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SCOPE SEMINAR

SZYMBARK SEPTEMBER 11-18 1991

Edited by
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Preface

The Szymbark seminar was held at the Szymbark Field Station of the Institute of Geography and Spatial Organization, Polish Academy of Sciences in the days 18-22 August 1991. The aim of this meeting was to analyse the information collected on terrestrial organic matter processes in a broad geographic scale.

The predicted change of the global climate will affect especially the terrestrial ecosystems of the temperate and northern zones. The belts of temperate and northern vegetation will move northwards; organic matter budgets in these ecosystems should change as the rates of such ecosystem processes as production and decomposition will be accelerated by higher temperatures. These changes can be predicted to some degree from presently occurring ranges of rates of these processes in different thermoclimates.

Comparative analysis of this type of ecological results enables realistic evaluation of natural variability of presently existing ecosystems on the Globe. The expected warming of climate on Northern Hemisphere fits the range of present thermic conditions on the Earth. Studying the behaviour of ecosystems in these ranges one can predict the eventual modifications caused in the inner structure/function of ecosystem by the change of climate or, at least, one can use these data in the modeling assumptions to correlate ecosystem-climate features.

Szymbark SCOPE seminar belongs to the series of meetings related to the realization of the SCOPE project on "Organic matter budgets in terrestrial ecosystems". The project originally entitled "Comparative ecology of terrestrial ecosystems: production/decomposition budgets" was proposed by signed below on behalf of Polish SCOPE Committee at VI SCOPE General Assembly. After some re-elaborations it was approved by SCOPE Executive Committee at its Delft meeting (November 11-12, 1987) under the title "Production/decomposition budget of organic matter". Alicja Breymeyer (Poland) and Jerry Melillo (USA) were invited to co-chair this project; Scientific Advisory Committee (SAC) of six was established including J.Landsberg, M. Swift, D. Hall, G. Agren and 2 co-chairing persons. After some time J.C.Menaut was invited to join SAC. IGBP — Global Change stimulated some re-shaping of the project to meet the expected global warming influence.

Beginning from 1989 several meetings were organized in the frame of the project:

— "Ecosystem response to climate change: the effects of climate change on

production and decomposition in coniferous forests and grasslands". Workshop at Woods Hole, USA, April 9-14.1989, hosted by Jerry Melillo, SAC member and co-chair person.

— Grasslands and forests modeling groups meeting, Woods Hole January 1990.

— "The effects of climate change on production and decomposition of coniferous forests and grasslands". Workshop at Kings College, London, September 17-22.1990, hosted by David Hall, SAC member.

— Grasslands modeling group meeting, Kings College, March 18-21.1991.

— "Geography of organic matter budgets in terrestrial ecosystems". Seminar at Szymbark, Poland, hosted by Alicja Breymeyer, SAC member and co-chair person.

The presented proceedings involve the information collected in broad scale networks and transects. Several global scale maps and numerous tabulations create additional value of this volume which, I hope, will satisfy our small group. Even more satisfying are news on development of the idea of organic matter budgets between ecologists: the new SCOPE project proposed by French SCOPE Committee "Tree-grass dynamics: driving forces and consequences on organic matter budgets" is accepted; English TIGER (Terrestrial Initiative in Global Environmental Research) involves the studies of organic budgets in various projects. I believe, that this is a fruitful way to face global changes in our planet.

Alicja Breymeyer

GLOBAL MAPS OF ORGANIC MATTER STRUCTURE IN TERRESTRIAL ECOSYSTEMS

ROMAN I.ZLOTIN, NATALIA I. BAZILEVICH

Abstract. Organic matter distribution through all continents was analysed for following reservoirs: humus, phytomass alive and dead, microorganisms, wild and domesticated animals and biomass of human population. Geographical patterns of different organic matter fractions are shown on the maps. The global structure of organic matter can be expressed as following row of OM fractions measured in 10^{12} kg: 2040 kg humus, 2400 kg phytomass, 600 kg mortmass, 20 kg microbial mass, 1.0 kg wild biomass, 0.3 kg domestic biomass, 0.1 homomass.

Key words: organic matter reservoirs, maps, models; global maps.

INTRODUCTION

The key issue in the problems of global environmental change is the carbon budget. The available quantitative assessments of carbon flows between reservoirs are still few and contradictory. It is noteworthy, however, that not only the flows intensity is disputed today, but even the general direction of the carbon flow is still uncertain. It is still not clear whether the biota is a source or sink for the atmospheric CO_2 (Kobak 1988).

There exist several assessments of global standing crop and structure of the organic matter (OM). Evaluations by different authors of the absolute values and ratios of OM amounts differ significantly but the general pattern is rather constant. Evaluations of OM storage which are produced by N.I. Bazilevich (1979) are an outcome of a synthesis of numerous publications and original calculations (Table 1).

Continents are the main reservoir of the OM. The terrestrial ecosystems concentrate over 98% of alive OM and nearly 30% of dead OM. A lot of the dead OM (44%) is buried in oceanic silts.

Huge amounts of dead OM are buried in geological layers; this is production of the past biospheres. The continental desposits are twice as big as the oceanic ones.

The main aim of this paper is presentation of OM distribution through all continents and in all reservoirs of OM. These reservoirs are: OM of soil (humus), vegetation (alive phytomass, dead phytomass or mortmass), microorganisms (microbialmass), animals, both wild and domestic (zoomass), biomass of man (homomass).

All maps demonstrated in this paper were developed in the Institute of Geography, Russian Academy of Sciences (IGRAS). IGRAS has the good traditions in thematic geographic mapping and acquired large empirical data bases of the OM distribution pattern in the terrestrial ecosystems.

Table 1. Global content of organic matter (OM) and organic carbon (C) in the earth reservoirs (after Bazilevich 1979)

Components of OM	OM in ton	C	
		bln. t.	in %
Alive OM, total	2429	975	100
Continents, total	2425	973	99.8
Phytomass	2402	961	98.6
Zoomass and microbialmass	23	12	1.2
Ocean, total	4	2	0.2
Phytomass	0.2	0.05	0.0
Zoomass and microbialmass	3.3	1.7	0.2
Dead OM, total	11060	5656	100
Continents, total	3262	1593	28
Humus	2042	1021	18
Mortmass	574	249	4
River alluvium	300	150	3
Peat	220	110	2
Sapropel	116	58	1
Others	10	5	0.1
Ocean, total	7791	4058	72
Slime (Holocene)	4456	2228	39
Dissolved OM	3275	1800	32
Weighed OM	60	30	0.5
Atmosphere, total	8	6	0.1
Dead OM in the geological sediments, total		15048	100
Continets		10000	66
Ocean		5000	33
Coal		30	0.2
Oil		2.5	0.0
Others		16	0.1

GEOGRAPHICAL PATTERN OF SOIL OM STRUCTURE

The main component of OM in soils is humus. The peat and organic debris of plant and animal tissue are an essential parts of soil OM also.

Humus usually accounts for about 90% of total OM in soils. It concentrates about one third of all alive and dead organic matter of terrestrial ecosystems. Assessments by different sources of total global storage of carbon in humus can frequently vary; this is because the authors use different data on organic carbon concentrations in the same soil types, and also take different areas for the same soil types. Kobak (1988) has studied 15 publications, mostly of Western authors, and has found that global humus storage ranges from $700 \cdot 10^{12}$ kg C up to $3000 \cdot 10^{12}$ kg C.

Amounts of organic carbon stored in humus are shown in Table 2 in accordance to different climatic zones and regions. The highest index of humus storage

is in the boreal zone (1/3 of the global sum), though this zone itself accounts for only 17% of total Earth surface. About 20% of humus are in the tropical zone (40% of surface of land). The subtropical and subboreal zones show a gradual reduction. The arctic zone has the lowest C storage (7%), but is next to the boreal zone in C concentration per area unit.

Table 2. Distribution of soil carbon in different thermic belts, geographical regions and biomes (after Kobak 1988)

Thermic belts, regions, biomes	Surface		C org. content		
	mln. km^2	%	$kg \cdot m^{-2}$	bln .t	%
TROPICAL	56.3	42.1	10.3	579	27.5
moist	25.9	19.4	13.5	349	16.6
draughty and dry	17.4	13.0	8.9	155	7.3
semidesert and desert	13.0	9.7	5.7	75	3.6
SUBTROPICAL	25.7	12.9	12.9	330	15.7
moist	6.5	20.3	10.3	133	6.4
draughty and dry	8.6	16.0	16.0	138	6.5
semidesert and desert	10.6	5.6	5.6	59	2.8
SUBBOREAL	21.9	16.5	14.6	320	15.2
forest	6.0	4.5	18.1	109	5.2
steppe	7.9	6.0	21.3	169	8.0
semidesert and desert	7.9	6.0	5.3	42	2.0
BOREAL	23.7	17.8	31.1	739	35.1
taiga	15.4	11.5	35.8	549	26.1
permafrost — taiga	8.3	6.3	22.6	190	9.0
POLAR	5.7	4.3	23.9	136	6.5
TOTAL	133.4	100	15.8	2104	100

Mapping humus storage in soil is a difficult task, because of the big diversity of soil types and of humus components. Hence, it turned out impossible to present on such a map the whole variety of the soil types that are in the FAO/UNESCO map (1987), where 106 soil types have been shown.

The map "Organoprofiles of natural soils of the world" was compiled by A.E. Cherkinsky and O.A. Chichagova (1991) in the Laboratory of Soil Geography of the IGRAS. It presents a distribution pattern of the types of "organoprofiles" — the term suggested by the Russian pedologist-ecologist L.A. Grishina (1986). Classification of organoprofiles of the natural soils in the World by A.E. Cherkinsky and O.A. Chichagova is based on several groups of diagnostic indexes: morphological, physical-chemical, and temporal (Table 3).

The morphological humus types correspond with classification of P. Duchaufour (1982): 1 — peat, anmoor — on-surface accumulation of weakly decomposed OM practically unaggregated with inorganic part of soil; 2 — moor, moder — accumulation of organic detritus on surface is less clear than in the previous type, humus is distributed in the profile by migration processes, it is weakly ag-

gregated with the mineral material; 3 — forest moder, mull — humus is predominantly accumulated within the profile, on-surface accumulation of organic matter detritus is low, humus is formed *in situ* as well as by migration processes, ions of iron, aluminium, and calcium aggregate it with the inorganic mineral substratum; 4 — steppe mull — soft humus formed *in situ*, strongly aggregated with the inorganic part of soil via calcium ions.

Features of the main types of global organoprofiles and their distribution pattern in the terrestrial biomes are shown in Table 3.

The accumulative-detrital type of organoprofile is formed in overmoistened conditions and is found mostly in the swamp ecosystems of the boreal and arctic zones, as well as of marsh areas. Radiocarbon age is several thousands of years (the Holocene), rates of decomposition, mineralization, and humification are low. High content of OM (humus + litter): up to 100 kg per sq.m.

The accumulative-detrital-humus type is associated with boreal coniferous forests high level of primary production, high litter biomass and eluvial water regime leading to the formation of intra-profile humus. Period of litter and humus regeneration is very short: few hundreds of years for litter and 2-3 thousand years for humus. Humus storage is moderate, 10-15 $kg \cdot m^{-2}$.

The accumulative-isohumus type occur under steppe vegetation and broad-leaved forests. High rate of plant fall humification, and low rate of humus mineralization. Period of litter regeneration is from several years to tens of years; the absolute age of humus is several thousands of years. Humus and litter storage is high: 15-30 $kg \cdot m^{-2}$.

Eluvial-illuvial-humus type occur under mixed forests with high amount of precipitation and moderate level of air temperature. Accumulation of OM is mostly in the upper soil horizons; high rate of humification. Litter and humus storage is 10-15 $kg \cdot m^{-2}$.

Eluvial-humus type occur under seasonal and wet rain tropical forests; very high year-round rate of decomposition, low content of humus: 5-10 $kg \cdot m^{-2}$, mostly in the upper horizons of the soil profile.

Mineralized-isohumus type is formed in the areas of sharp seasonal type of climate with one and more dry seasons — steppes and dry subtropical forests. Humus storage is low — 5-10 $kg \cdot m^{-2}$.

Low-humus type is formed in the area where one or several factors are strongly limiting vegetation. Humus and litter storage is below 5 $kg \cdot m^{-2}$.

The global map of distribution pattern of organoprofiles was compiled on the basis of the "World Soil Map", edited by V.M. Fridland and M.A. Glazovskaya, 1982. The total number of contours of organoprofiles identified in the world soil cover is over 150, the map is availabe in IGRAS, Moscow.

Table 3. The characteristics of the main organo-profile types (after Cherkinsky, Chichagova 1991)

Type of organo-profile	Humus, litter, $kg \cdot m^{-2}$	OM distribution in profile	Type of humus			Ecosystems
			Morphotype	C humic/ C fulvic	C/N	
Accumulative – detrital	above 30	shallow	peat, moor	0.3-1	above 20	bogs, wet tundra
Accumulative detrital – humus	10-15	shallow inside-profilic, sharp decreasing with depth	moor moor-moder	0.05-1	14-17	wet tundra, boreal forest
Eluvial – illuvial – humus	10-30	inside-profilic, bimodal, proportional decreasing	moder mull	0.2-2	10-15	temperate and subtropical forest
Accumulative – isohumus	10-30	inside-profilic, proportional decreasing	mull	1	10	steppe, savannas, subtropical moist forest, temperate forest
Eluvial humus	5-10	inside-profilic, sharp decreasing with depth	moder	0.5	20	tropical and subtropical rain and moist forest
Mineralized– isohumus	5-10	same	mull	0.5-2	10	dry steppe, subtropical & tropical forests
Low – humus	lower	dispersal, proportional decreasing	moder	0.3-1	10	semidesert, desert

GLOBAL STRUCTURE OF STANDING CROP AND PRODUCTIVITY OF OM IN THE "VEGETATION" RESERVOIR

In the terrestrial ecosystems the plant matter occurs in two forms — alive and dead. The alive matter (or phytomass) accounted for over 40% of total terrestrial storage of OM. Dead plant matter (or mortmass) is only 6% of the global terrestrial OM.

N.I. Bazilevich has carried out mapping of standing crop and production of phytomass and mortmass in the terrestrial ecosystems using a global data base, which is prepared in the Laboratory of Biogeography of IGRAS under her surveillance for about 500 sites. Each site has published data or original evaluated data on the standing crop structure of phytomass and mortmass, and primary production of OM. All assessments of primary productivity were carried out with unified techniques and methods (Bazilevich and al. 1978).

The maps of phytomass, mortmass, and annual primary production (Figs. 1, 2, 3*) were compiled on the basis of the global map of potential vegetation, and cover over 200 categories of plant formations (Physical-Geographical Atlas of the World, 1964). All indexes consist 10 categories of biomass from minimal to maximal ones (see Table 1 in paper of Bazilevich, Drozdov, Zlotin published in this volume).

Geography of standing crops of phytomass and mortmass and of primary production follows generally the same pattern. First, they are maximal in the tropical and subtropical thermal zones, and in the oceanic and suboceanic sectors of continents. Minimal indexes are registered for the arctic and subarctic zones, for regions with sharp and extreme continental climates, and also in subboreal, subtropical and tropical deserts. Second, the areas of high mortmass accumulation are clearly situated in high latitudes, unlike the areas of high phytomass storage and maximum primary production that are situated in the tropical or temperate latitudes.

The map of primary production compiled by N.I.Bazilevich (Fig.2) and the world maps of radiation balance (R gr $J \cdot m^{-2} \cdot y^{-1}$) (Uchijima, Seino 1987) and radiation drougth index (Henning, Flohm 1977) were used by Varlygin to establish the correlations of phytomass annual production indexes with the solar radiation factors (Varlygin, Bazilevich 1992). The conclusion was that the maximum values of production in each thermal belt do not form linear graphs, as it was assumed before (Bazilevich et. al., 1978; Efimova 1976), but form a broken line with an extremum of R within 1.5-2.0 and of drought index (R/Lr) from 1.0 to 1.5 located in the subboreal belt roughly between broad-leaved forests and the forest-steppe zone (compare Varlygin, Bazilevich 1992).

It was also confirmed that in all regions of the boreal, subpolar, and polar belts with the exception of arid ones, primary production of the zonal ecosystems increases with the rise of heat inflow, while in deserts the tendency is inverse. In the subboreal, subtropical and tropical belts primary production increases with moisture increasing.

An important conclusion for prognosis of the position of the natural zones in response to global climate change is that changes in radiation balance lead to

* All figures of this article are enclosed at the end of the volume.

shifting of the zonal boundaries. The shift becomes significant in the polar belt if radiation balance changes by 0.1 grJ · m^{-2} · y^{-1}, in the boreal belt — by 0.2. The corresponding increase of primary production is 1.5-2 times. In other thermal belts changes are visible if R goes up by 05.-1.2 grJ · m^{-2} · y^{-1} with increasing production about 1.2 times.

Varlygin (Varlygin, Bazilevich 1992) has suggested 4 hydrothermal areas (Table 4) that can be usefully employed for modeling dynamics of primary production on global level with the above discussed climatic parameters: radiation balance and radiation drought index.

Table. 4. Global hydrothermal areas (after Varlygin, Bazilevich 1992)

#	Areas	R	R/Lr	R/LE	Evaporation mm	Primary production t · ha^{-1} · y^{-1}
1	Sufficient moistening, insufficient warming	<1.5	<1	<2.1	100-550	<14
2	Sufficient moistening, sufficient warming	>1.5	<1.5	<2.1	>550	14-30
3	Insufficient moistening, sufficient warming	>1.5	1.5-7	2.1-6	200-550	4-20
4	Limited moistening, surplus warming	>2	>7	>6	<200	<4

Other parameters important for modeling the OM changes in the "Vegetation" reservoir are distribution of standing crop and production of phytomass in the main terrestrial biomes. Let us take for this purpose the assessments produced by K.I. Kobak (1988) using generalized data of Ajtay and Co. 1979, Olson 1963, Olson 1983, — Table 5. According to these calculations, the maximum standing crop and production of OM phytomass are in tropical rain forests, they are high enough in savannas and in boreal forests, and also in forests of the temperate zone and open woodlands.

Table 5. Carbon (C) storage in the Phytomass (Phm), Annual Net Primary Production (NPP) and carbon mobility (NPP/Phm) in the main terrestrial biomes (after Kobak 1988)

BIOME	Square		Phm		NPP		NPP/Phm
	$10^{12}m^2$	%	$10^{12}kg$	%	$10^{12}kg$	%	
Tropical rain forest	11.2	7.5	178.6	32.0	9.9	16.5	0.06
Tropical monsoon forest	5.1	3.4	44.6	8.0	3.2	5.3	0.07
Temperate zone forest	7.8	5.2	76.6	13.7	4.7	7.8	0.06
Boreal forest	10.6	7.1	111.6	19.9	3.4	5.7	0.03
Open forest	8.6	5.8	40.5	7.2	4.6	7.7	0.11
Savanna	23.5	15.9	57.6	10.3	14.2	23.6	0.25
Steppe	10.9	7.3	10.0	1.8	3.5	5.8	0.35
Tundra, alpine meadows	11.6	7.7	9.5	1.7	1.3	2.2	0.14
Desert, semidesert	39.3	26.4	6.5	1.2	1.4	2.3	0.22
Cultivated lands	14.6	9.8	12.5	2.2	9.4	15.7	0.75
Bogs	3.2	2.2	11.5	2.0	4.0	6.7	0.35
Lakes, streams	2.6	1.7	0.5	0.1	0.4	0.7	0.80
TOTAL	149.2	100	560	100	60	100	0.11

MICROORGANISMS RESERVOIR

Data on geography of density and biomass of microorganisms, i.e. bacteria and fungi are rather fragmentary. These parameters were defined for some types of ecosystems and zonal biomes in the period of research under the International Biological Programme. This is sufficient for the preparation of the so-called general "OM formula" (e.g., see French et al., 1979) for selected ecosystems, but not enough for global mapping of the microbe biomass and microbiological processes. The "OM formula" states the ratio of OM amounts in the following reservoirs — humus, phytomass, microbialmass and zoomass. Hence, this OM formula in oak-forest of the forest-steppe zone of the temperate belt is 1600:500:8:1, and the same for meadow steppe is 1800:100:5:1.

The main pool of microorganisms is associated with soil. An integrated indicator of activity, and consequently, of density of microorganisms can be provided by CO_2 output from soil to atmosphere, if we identify in this flow the microbiological component. The available data, though fragmentary, allow for such an attempt. One can assume that microorganisms account for about 30% in the total CO_2 flow from soils (Coleman 1973; Zlotin, Khodashova 1980).

Total CO_2 flow from soil surface is presented in Table 6. One can notice that the range of fluctuations is small: 3-7 times from zonal tundra and desert soils to soils of humid tropical forests. Given the energy equivalent of CO_2 and P/R ratio in microorganisms, one can approximately assess the amounts of global microbe biomass and production: they are 20 and 60 kg·10^{12} respectively.

Table 6. Global CO_2 flow from soil surface (after Kobak 1988)

SOIL	Square %	CO_2 output $kg.ha^{-1}.day^{-1}$	CO_2 output duration days	CO_2 flow 10^{12} kg C per year
Podzol	9	50-80	150	6.7
Chernozem, tropical black soil	6	100-130	150-200	12.4
Gray and brown forest soil	7	40-80	150	6.8
Chestnut soil, red-brown soil	7	40	150	4.6
Desert	17	5-10	200-300	2.5-3.8
Red soil, laterit	19	150	360	17.5
Alluvial	4	60	200	1.0
Mountain	16	5-33	150	1.8
Tundra	4	20	50	5.9
Glacier	11	-	-	-
TOTAL	100			60

Herewith listed are also parameters of the microbe biomass in some types of zonal ecosystems evaluated by the experimental technique of direct count (Table 7).

Table 7. Microbial biomass [g per sq.m] in zonal types of soil of the former USSR (after Mirchink, Panikov 1985; Parinkina 1989)

Zone, site, soil	Fungi	Bacteria
Tundra, moss-sedge-bush, tundra gley soil, Yakutia	98.1	no data
Tundra, dryas-sedge-moss, tundra gley soil, Taymyr peninsula		
spot	50.3	41.8
border	73.4	7.5
Taiga, boreal picea forest, soddy podzolic soil, Novgorod distr.	377.2	37.3
Mixed forest, temperate picea-herbs forest, soddy podzolic soil, Moscow distr.	202.6	40.5
Forest-steppe, chernozem soil, Kursk distr.		
meadow steppe, reserve	157.7	94.0
meadow steppe, mowed	79.5	66.7
oak forest	124.2	47.0
Moist subtropical forest, beech-hornbeam-hardwood forest, red soil, Adjaria, Caucasus	111.0	18.5
Subtropical sandy desert, Haloxylon woodland, sandy desert soil, Repetek Biosphere Reserve, Turkmenia	24.6	5.0

GLOBAL STRUCTURE OF WILD ANIMALS BIOMASS

Global assessments of the biomass of animal populations are very rare. The only source of information is data based on all zoomass components compiled by our own during the recent 20 years. These materials are mostly original ones. Besides, all available published information on individual components of zoomass was used.

Table 8 shows the data on zoomass structure arranged by the main types of the world zonal ecosystems. We have discovered a close correlation of total zoomass and its individual components with other OM components (Chernov, Khodashova, Zlotin 1967; Zlotin 1975). Emphasis should be placed on the fact that the correlation of zoomass with phytomass and primary production, and of the members of trophic chains (e.g., phytophagans and primary production, saprophagans and plant fall, predators and their prey, etc.) is very strong. Thus, it is possible to assess the different components of zoomass with data on other components of OM.

This data base was used to produce a global map of zoomass for a potential ecosystems cover (Fig.4). In accordance with the available information, we have took as the basis the global vegetation map including 28 categories of plant cover. The plant formations representing habitats of animal populations are classified as the northern hemisphere, southern hemisphere and the tropical zone, mountains and lowlands. Thus, all thermal belts and biomes are represented.

5 categories (or levels) of zoomass have been identified — from very low ones (less than 10 kg per ha) to very high ones (over 240 kg per ha). Besides, determined was one group of habitat that practically has no zoomass (glaciers). The group of very low zoomass includes high-latitude, cold and hot deserts, mountain deserts and mountain tundras. Maximum zoomass is found in broadleaved forests within the temperate and subtropical belts mostly of the northern hemisphere.

Table 8. Zoomass structure in some zonal biomes

BIOMES	Zoomass* $g \cdot m^{-2}$ dry weight	% of total zoomass									
		inver-tebrates	verte-brates	under-ground	above ground	meso-fauna	micro-fauna	nema-tods	sapro-phags	phyto-phags	zoo-phags
Arctic tundra (1)	3.0	98	2	97	3	7	78	15	97	1	2
Taiga (2)	8.0	97	3	95	5	89	8	3	98	1	1
Broad-leaved oak forest (3)	32.1	99	1	99	1	96	3	1	96	3	1
Tropical rain forest (4)	13.3	98	2	96	4	93	4	3	92	4	4
Temperate grasslands											
meadow steppe (5)	31.5	98	2	96	4	93	1	6	95	4	1
true steppe (6)	8.3	97	3	88	12	85	10	5	77	20	3
dry steppe (7)	5.8	93	7	90	10	62	20	18	72	24	4
Semidesert (8)	1.3	63	37	58	42	57	12	31	22	73	5
Subtropical savanna (9)	5.4	92	8	88	12	69	25	6	21	74	5
Temperate desert (10)	0.2	87	13	71	29	34	29	37	68	22	10

* – without protozoans

1 – Norway, Svalbard (Zlotin, 1984a); 2 – Russia, Novgorod dstr., Valday (Glazov, 1979), 3 – Russia, Kursk dstr., Central-Chernozem Zapovednik (Zlotin, Khodashova, 1980); 4 – Fiji, Viti-Levu J. (Zlotin, 1975); 6 – Ukraine, Streletzkaya steppe Zapovednik (Zlotin, 1975); 7 – Ukraine, Askania Nova Zapovednik (Zlotin, 1975); 8 – Kazakhstan, Dzhanybek LSFR Station (Zlotin, 1975); 9 – Turkmenia, Mary dstr., Badhyz Zapovednik (Zlotin, 1984b); 10 – Uzbekistan, Bukhara dstr., Kyzyl-Kum desert (Gruznova, Domnikov, Zlotin 1984).

Most of northern hemisphere area is characterized by medium level of zoomass, in tropics and in southern hemisphere the areas with low zoomass prevail.

The preliminary assessment of total global zoomass carried out with this map is about $1.1 \cdot 10^{12}$ kg. The actual zoomass values of the current ecosystem cover is lower by about 20% due to of anthropogenic transformation of ecosystems. Currently, about 30-40% of land surface is being transformed by economic activities in different scales (Krenke 1989).

As a general rule, the zoomass structure is absolutely dominated by invertebrate saprotrophic animals inhabiting the soil stratum and this is repeated in humid ecosystems independently of their thermic condition. The biological cycling in these ecosystems is of detritus type and is realized by the saprotrophic organisms.

Arid ecosystems (steppes, savannas, deserts) are characterized by a high proportion of above-ground zoomass (up to a half and more of total zoomass), including the vertebrates. The role of herbivores is significant; therefore, the biological cycle acquires the so-called "grazing" type.

Summing up the brief analysis of the global map of zoomass, one should emphasize that the carrying capacity of this reservoir is more dependent on the biotic factors, i.e. on the level of production of the OM components, than on the climatic factors. The correlation of the zoomass level with climatic factors in the zonal biomes is indirect, via the primary and secondary production.

GLOBAL STRUCTURE OF DOMESTIC ANIMALS BIOMASS

Economic activity and land use significantly modified the biomass structure of wild animals and reduced its global value. These losses were compensated by the biomass of domestic animals showing a trend to a constant growth. According to FAO data of the end of the eighties, the global biomass of domestic animals oscillates about $0.3 \cdot 10^{12}$ kg. This is 3-4 times less than the potential wild zoomass, or 2-3 times less than its real current value.

The major part of biomass of domestic animals is that of cattle — about 35%, and of pigs — 30%.

We have compiled a map of distribution of the biomass of domestic animals (DA) as a first such attempt. We know the computer global maps of stock of different DA produced by NASA Goddard Space Flight Centre for evaluation of zoogenic methane emission to atmosphere. Our map is based on recent FAO data (Fig.5). The cartographic base of the map is the World Political Map with administrative boundaries of states, provinces, or regions of countries. Unfortunately, it was impossible yet to get detailed information on distribution of DA within some countries. We are currently developing a more accurate version of DA biomass map with the same gradations of biomass, as on the map of biomass of wild animals.

An analysis of this map suggests some general conclusions. First, unlike the geography of wild animals, that of DA is a driven by the socio-economic not by natural factors. The cattle-breeding and its geography have certain historical traditions. One can observe that by the levels of the DA biomass the countries

are differentiated into the developed and developing ones; with very low DA level in poor African countries, and high in Western Europe. Second, mean global level of biomass of DA is by about 1 rank below the biomass of wild animals. Third, one can trace certain geographical patterns of DA biomass by continents. In the western hemisphere the biomass is generally low. In Africa about one half of the territory has a low biomass, and the other half — a very low one. Very low DA biomass occurs in Australia, but in the eastern, more populated part of this continent the biomass is one rank higher.

Large amplitude of DA values is observed in the European countries — from very high to very low biomass, the average level is medium-high. The second region with a very high DA biomass concentration is the south-eastern Asia and India. Eastern Europe and Western Siberia have mostly low biomass, and the arctic, boreal and temperate zones of Asia — very low biomass.

GEOGRAPHY OF BIOMASS OF THE HUMAN KIND (HOMOMASS)

The last important reservoir of OM on our planet is the *Homo sapiens* population. According to the eloquent words of V.I. Vernadsky: "The humanity has become a geological force", it now influences the development of the planet no less, than the natural factors. The Earth is at a threshold of global changes provoked by human economic activities.

5 billions inhabitants of the Earth amount to $0{,}1 \cdot 10^{12}$ kg, which is almost comparable with the DA biomass and only 10 times less than total biomass of wild animals (WA). The ratio of homomass and WA biomass is extremely low: if one assumes that man is mostly a predator, the ratio of his biomass to the biomass of his prey should be 1:100-200. Otherwise, the reproductive potential of the prey is undermined, and this is what is actually being observed. The function of animals, (including man), as heterotrophs is controlling the ecosystem processes, and the production-destruction equilibrium. In view of the technological power of humanity and its aggression to nature, as well as the rather low level of its environmental culture, the future of the biosphere arouses grave concern.

The map of homomass distribution (Fig.6), similarly to the maps of biomass of wild and domestic animals, depicts geography of the biomass in 6 categories. The map is compiled on the basis of the map of population density in the eighties, with particular attention to differences of mean body weight and age structure of the population.

One can easily notice a good agreement of the contours on the homomass map and on the map of DA biomass, and also, though to a smaller extent, on maps of productivity of the potential vegetation and of biomass of wild animals. This correlation is especially clear in the Old World. In the western hemisphere concentrations of homomass are associated with settlement contours, being attracted, in particular, to the coastal zone. The continental sectors of North and South America are significantly less populated. Maximum homomass is observed in south-eastern Asia and Europe, i.e. in the areas of ancient civilizations.

FORMULA OF OM

The global structure of OM can be represented by its ratio in all reservoirs, arranged in the order of reduction of OM amounts:

humus : phytomass : mortmass : microbialmass : wild zoomass : domestic zoomass : homomass

$$2040 : 2400 : 600 : 20 : 1.0 : 0.3 : 0.1 \times 10^{12} \text{ kg} \quad (1)$$

If one tries to interpret the structure of annual OM increment as its ratio in all reservoirs, the formula will become as follows:

humus : phytomass : mortmass : microbialmass : wild zoomass : domestic zoomass : homomass

$$5 : 120 : 130 : 60 : 1.5 : 0.2 : 0.02 \times 10^{12} \text{ kg} \quad (2)$$

The transformation of formula 1 into formula 2 is explained by different rates of OM regeneration in different reservoirs.

The rates of the production and destruction processes follow their own patterns, they change in accordance with the hydrothermal and socio-historical factors. The latter refers to the reservoirs of DA and homomass.

According to assessments of Kobak (1988) with our amendments, the rates of regeneration of litter in the mortmass reservoir, decrease from the tropical to the polar thermal zones in the following way: tropical zone — 0.5 year, subtropical — 1-2 years, subboreal — 2-3 years, boreal — 10-20 years, polar — 25-50 years.

In conclusion, in order to define the global budget of carbon and its dynamics under climate and land use change, it is necessary to produce a reliable assessment of the OM amounts and it production in all reservoirs for the current ecosystems cover.

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SOIL CARBON DIOXIDE EVOLUTION: ENVIRONMENTAL CONTROLS, WORLD PATTERNS AND AMOUNTS

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Abstract. The general relationships between climate and soil CO_2 evolution, major flux in the global carbon budget, are analysed. The models predicting world-wide CO_2 evolution are proposed. Actual evapotranspiration (AET) was used as a measure of simultaneous supply of warmth and wetness to the site. The data-base of 48 sites represents all main world climate types. Temperature and AET seems to be the primary controls of soil CO_2 evalution.

Key words: CO_2 evolution, global maps, AET, predictive models.

INTRODUCTION

The flux of carbon dioxide from the soil surface to the atmosphere, called soil CO_2 evolution, is a major flux in the global carbon budget. It involves both biotic and abiotic processes. Soil CO_2 evolution and autotrophic respiration together account for most of the CO_2 returned by natural processes to the atmosphere from the Earth's land areas. Other natural carbon fluxes from land involve physical and anaerobic processes and other carbon species. Better estimates of the determinants, amounts, and geography of these processes are needed.

The study of CO_2 evolution began with the pioneer work of E.G. Russell and A. Appleyard (1915), H. Lundegårdh (1924, 1927), and L.G. Romell (1927). CO_2 evolution has been studied from the perspective of soil microbial processes (Macfayden 1970, Billes et al. 1971, Upadhyaya and Singh 1981), root respiration (Wiant 1969, Coleman 1973, Anderson 1973, Herman 1977), soil chemical properties (Jorgensen and Wells 1973), and carbon balance (Lieth and Ouellette 1962, Reiners 1973b, Edwards and Harris 1977, Schlesinger 1977). Other studies have examined soil moisture and temperature control over CO_2 evolution rates (Witkamp 1966a, 1966b, Wiant 1967a, 1967b, Wildung et al. 1975, Edwards 1975, Kowalenko et al. 1978), the CO_2 content of the soil atmosphere (Brook et al. 1983), and the role of soil CO_2 in denudation of karst landscapes (Drake 1980). J.S. Singh and S.R. Gupta (1977) have reviewed additional factors which affect respiration rates, especially in agricultural settings.

Soil CO_2 evolution, sometimes called "total soil respiration," is derived from at least four sources: 1) decomposition of soil and surface organic matter (detritus) by soil microorganisms and animals; 2) respiration by living roots; 3) abiotic loss of CO_2 from warming soil water, displacement of soil CO_2 by water, and barometric pressure changes; and 4) some photorespiration, depending on measurement procedures (Billings et al., 1977). Most of these processes are directly or indirectly controlled by temperature and moisture. Correlations between CO_2 evolution and these factors have often been investigated at specific sites (e.g. Reiners 1968).

The purpose of this study is to determine the general relationships between climate and CO_2 evolution, and to produce a predictive model of CO_2 evolution which could be used world-wide to produce an initial geographic inventory of CO_2 evolution. A regional geographic model of detrital decomposition rates based on climate was produced by V. Meentemeyer (1974), and global inventories have been done for various carbon-balance components such as primary productivity (Lieth and Box 1972, 1977), soil carbon (Meentemeyer et al. 1982, 1985), and soil CO_2 content (Brook et al. 1983). Climatic variables worked well as predictors of such phenomena, at least at world scale. Soil CO_2 evolution, however, is more intimately involved with soil and topographic factors, and the environmental relationships appear to be much more complex. This complicates the construction of a general model; more mechanistic details and more environmental data are needed. As a result, this study developed over several years. Nevertheless, the goal remains to provide insight and initial global estimates of CO_2 evolution amounts and geography. These results can be compared with estimates of net primary production and total litterfall to refine estimates of the storage and fluxes of terrestrial carbon and its broad-scale geographic patterns.

CO_2 EVOLUTION AND SITE CONDITIONS

Working on sites with little variability in soil moisture, W.A. Reiners (1968), N.T. Edwards (1975), and Y. Takai et al. (1977) found strong correlation between soil and/or litter temperature and soil CO_2 evolution. At sites with considerable moisture stress, E. De Jong et al. (1974), in a Canadian prairie, and E.D. Schulze (1967) in the dry season in Costa Rica, found the strongest statistical relationships with soil moisture rather than temperature. J.E. Cowling and S.F. MacLean (1981) found that soil respiration in a black spruce (*Picea mariana*) forest in Alaska was negatively correlated with soil temperature during the frost-free season and positively correlated with soil moisture. For an oak-hickory (*Quercus-Carya*) forest in Missouri, H.E.Garret and G.S. Cox (1973) reported that, "The influence of soil moisture on the released CO_2 was obscured since it was confounded with the effect of temperature." Thus, depending on the degree of moisture stress, soil CO_2 evolution may be controlled by temperature or by soil/litter moisture or by interactions between these factors.

R.E. Wildung et al. (1975), working in an arid shrub-steppe in Washington, found CO_2 evolution to be described best by a soil temperature-soil water interaction term. E. De Jong et al. (1974), however, found that "... the number of wetting and drying cycles in the soil was mainly responsible for the annual variations in soil respiration." They believed that soil CO_2 evolution in the Canadian prairies can exceed net primary production in wet years, and that the reverse is true in dry years. Data collected by E. Fouseki and N.S. Margaris (1981) for phrygana (mediterranean shrublands) in Greece showed CO_2 evolution rates higher for a dry year than for a preceding wet year.

J.E. Cowling and S.F. MacLean (1981) found precipitation events to stimulate CO_2 production and extended periods of dry weather or rainy weather to retard CO_2 production. R.C. Ellis (1969), working in a *Eucalyptus* forest in Australia, believed "precipitation increments" to be more important than soil moisture in predicting CO_2 evolution (cf. Birch 1968).

In general, the literature suggests that soil CO_2 evolution has a Q_{10} (exponential) relationship with temperature, with Q_{10} values ranging from 1.6 to 3.2 (Schlesinger 1977). At some sites, Q_{10} values as high as six have been found, especially at higher latitudes (Schleser, 1983). Moisture control seems to possess primarily upper and lower thresholds, where CO_2 evolution is retarded by a lack of capillary film needed by decomposer organisms, or by waterlogging, which restricts oxygen availability. At moisture levels from 100 to 250% of dry weight for the L and F layers of spruce forests in Alaska, J.E. Cowling and S.F. MacLean (1981) found that CO_2 evolution increases with moisture content. The optimum moisture content was between 200 and 250%.

Virtually all site-specific studies of soil CO_2 evolution have found an exponential relationship with soil or air temperature, especially when the soil is neither very dry nor waterlogged. K. Van Cleve and V. Alexander (1981) found a strong exponential relationship between mean annual temperature and soil CO_2 evolution rates at sites with mean annual temperatures below 10°C. This temperature relationship follows the law of Van't Hoff and Arhenius, as do various other processes (e.g. autotrophic respiration), but will be bounded by moisture shortages at many of the warmer places on earth, producing great differences in CO_2 evolution for a given mean annual temperature. Since both litter production (Meentemeyer et al. 1982) and decomposition rate (Meentemeyer 1974, 1978) increase with increasing actual evapotranspiration (AET), it seems reasonable to expect that CO_2 evolution may also increase with increases in this useful interaction variable AET, a measure of the simultaneous supply of warmth and wetness.

The environmental models produced by the above authors are site-specific and cannot be used worldwide. The results, however, suggest that the combined effects of moisture and temperature may be used to produce a general climatic model, based on full-year CO_2 evolution data as well as climatic data, from as many experimental sites worldwide as possible.

MEASUREMENT OF SOIL CO_2 EVOLUTION

When our study began (1981), three general methods had been developed for measuring CO_2 evolution in the field:

1. a "theoretical" method, by which CO_2 is measured in the soil profile and CO_2 evolution is estimated based on CO_2 gradients and theoretical diffusion equations (e.g. De Jong and Schappert 1972).

2. a "dynamic" method, which uses some type of gas analyzer (often infrared) to monitor the flow of air through an inverted box (e.g. Edwards 1975, Reiners 1968, Schleser 1983).

3. a "static" or alkali-absorption method (Haber 1959, Macfadyen 1970), in which a dish of KOH or (NaOH) is placed inside a chamber or inverted cylinder driven into the soil, with the absorbed CO_2 then determined by titration.

Sometimes a vacuum is applied in the dynamic method, and flow rate may be a problem with this method (Reiners 1968, Schwartzkopf 1978). CO_2 detection at the lowest flow rates possible is important so that CO_2 evolution will not be overestimated (Schleser 1983). The most common method, the static method using KOH, is simple but may understatement the amount of CO_2 evolved, especially if more than 20% of the alkali is neutralized (Kirita and Hozumi 1966, Haber 1959) claimed that the KOH method gives values of only 75% + 4.65% of the actual respiration rate and suggested adjustment of such results by multiplying by the factor 1.33. As a result, many studies using this method routinely "adjust" the results accordingly (e.g. Wanner et al. 1973).

These measurement methods were compared and evaluated by V.N. Mina (1962), A. Macfadyen (1970), and E. De Jong et al. (1979). A. Macfadyen warns against stimulation of CO_2 evolution by the operator, and J.E. Cowling and S.F. MacLean (1981) warn against altered arthropod density and soil moisture and temperature inside cylinders. W.A. Reiners (1973b) suggests that relationships between soil temperature and CO_2 evolution may in part be caused by the increased diffusion rates at higher temperatures and not by increased microbial activity. These studies in general support underestimation by static, alkali-absorption methods.

THE CO_2 EVOLUTION DATA-BASE

To estimate CO_2 evolution worldwide, data are needed from as many different climatic and ecosystem types as possible. Review articles by W.H. Schlesinger (1977), J.S. Singh and S.R. Gupta (1977), and K. Van Cleve and V. Alexander (1981) provided many references. It became readily evident, however, that many of the data reported could not be used because of extremely short measurement periods, unusual situations, because the data were collected in a laboratory or on plants grown in boxes, or for other reasons (e.g. Minderman and Vulto 1973, Salonius 1978). Annual CO_2 evolution, when not given by the authors, could

sometimes be read from graphs or tables, or acquired by contacting the authors. In some cold environments, CO_2 evolution was not measured during the winter but could be assumed to be near zero at this time, although various authors report that some CO_2 can be evolved through a snow cover (e.g. Kelley et al. 1968).

Data from studies up to 1983, based on all forms of measurement, were collected to produce an initial data-base of 34 sites. The dynamic methods showed much higher values than those based on static methods, but there is reason to believe flow-based measurements may be more accurate. The KOH method was the most common and apparently the most consistent from site to site and author to author. We use both types of data and adjust the static-method values by 1.33, as suggested by W. Haber. Where multi-year data were available for a site, these were averaged to produce a single annual value. Similarly, values for different but similar sites at the same station were also averaged, unless the vegetation cover was different.

Monthly temperature and precipitation data were also obtained or estimated for each of the sites with useable soil CO_2 evolution data. Several studies reported site temperature and precipitation during the measurement period, plus some climatic data from a nearby station. In other cases monthly climatic data during the measurement period were obtained from C.J. Willmott et al. (1981a, 1981b) for two or three surrounding stations. The site climate was then estimated by customary interpolation and triangulation procedures. At some sites the weather data for the time of measurement were not available, so average monthly values were refined from an available computerized world climatic data-base (Box 1981) or from C.J. Wilmott et al. (1981a). Monthly water-balance variables (potential and actual evapotranspiration, soil moisture surplus and deficit, etc.) were calculated from the primary climatic data, based on the procedures developed by C.W. Thornthwaite and J.R. Mather (1957). To test the effects of seasonality on CO_2 evolution, the seasonal ranges of mean monthly temperature and precipitation were included, since these have already been related to CO_2 evolution (Schlesinger 1977) and to litter production (Bray and Gorham 1964), a source of carbon for CO_2 evolution.

This data-base of 34 sites was used for some initial statistical analyses. Tropical situations, however, were not well represented, especially the possibility of low CO_2 evolution over large tropical areas, as suggested by some low CO_2 values measured at humid tropical sites (e.g. Wanner 1970, Medina et al. 1980). As a result, more tropical data were sought. Fourteen measurements were added, mostly tropical, including both long-term studies (Anderson et al. 1983) and very short-duration measurements (Wanner et al. 1973); some involved more unusual topographic situations (e.g. floodplains, coastal strand, gley) and/or vegetation (e.g. "heath" forest). This yielded a total data-base of 48 sites, but without averaging the additional, tropical sites, in order to represent better the different edaphic and/or topographic situations involved.

For each site in this world data-base (n=48), the soil type and A-horizon soil pH were recorded (if provided) or estimated from FAO (1974) and other soil maps and descriptions. Vegetation/landscape type and topographic situation were

Table 1. Soil CO_2 evolution sites, data and sources

Site	Country	Latitude	Elevation	Climate	AET	Vegetation	Measuring method	Measuring duration	Raw CO_2	Adjusted CO_2	Source
Pasoh	Malaysia	3.0°N	110	I	1548	rainforest	S	1 year	5212	6932	Ogawa 1978
Khao Chong	Thailand	9.0°N	160	I	1642	rainforest	S	19 days	5422	7212	Yoda & Kira 1969
Ariuau (Amazonas)	Brazil	1.4°S	40	I	1512	rainforest	S	2 weeks (August-September)	1060	1410	Coutinho & Lamberti 1971
San Carlos de Negro	Venezuela	1.2°S	119	I (seasonal)	1295	laterite forest podzol forest (tall Amazon caatinga)	S	2 1/2 years	753 1089	1002 1449	Medina et al. 1980
Gunung National Park	Sarawak	4.0°N	170	I	1584	heath forest	S	1 year (bimonthly)	2689	3576	Anderson, Proctor Vallack 1983
			50		1620	alluvial forest	S	1 year (bimonthly)	1629	2167	
			250		1575	dipterocarp forest	S	1 year (bimonthly)	2120	2820	
			300		1470	forest on limestone	S	June & August	2317	3082	
Bako National Park	Sarawak (coastal)	1.5°N	26	I	1698	dipterocarp forest heath forest		5 days 5 days (June)	1805 1666	2400 2216	Wanner et al. 1973
Pangandaran Nature Reserve	S. Java	7.7°S	13	I	1525	rainforest strand forest	S	3 days (April)	1286	1710	Wanner et al. 1973
Tjibodas (Java)	Indonesia	6.8°N	1400	I (montane)	835	mtn. rainforest	S	2 weeks	1679	2233	Wanner et al. 1973
Rancho Grande	Venezuela	9.0°N	1126	II (montane)	801	cloud forest	S	1 year	788	1048	Medina & Zelwer 1972
Calabozo	Venezuela	9.0°N	150	II	1281	forest patches in savanna	S	1 year	2190	2913	Medina & Zelwer 1972

Site	Country	Latitude	Elevation	Climate	AET	Vegetation	Measuring method	Measuring duration	Raw CO_2	Adjusted CO_2	Source
Baluran Nature Reserve	E. Java	7.8°S	930	III	855	grassland savanna grove	S	10 days 4 days (May)	1416 1554	1883 2067	Wanner et al. 1973
Kurukshetra	India	30.0°N	250	II	722	grass	S	1 year	1633	2172	Gupta & Singh 1981
Ujjain	India	23.2°N	492	II	928	grass	S	1 year	2297	3055	Upadhyaya & Singh 1981
Chakia/Varanasi	India	25.0°N	350	II	973	deciduous forest	S	1 year	1174	1561	Singh 1979
Rouquet	France	43.7°N	180	IV	700	oak woodland	S	3 years	1552	2064	Billes et al. 1971
Mt. Hymettus	Greece	38.0°N	400	IV	343	phyrgana	S	2 years	1386	1843	Fouseki & Margaris 1981
Monte Taburno	Italy	41.1°N	1050	IV (montane	542	beech forest	S	14 months	1168	1553	Virzo De Santo 1976
Tifton/Georgia	U.S.A.	31.5°N	113	Ve	991	crops	S	1 year	3312	4405	Hendricson 1981
Melbourne/ /Victoria	Australia	38.0°S	5	Ve	700	eucalyptus	D	15 months	3444	3444	Ellis 1969
Landsburg/Wash.	U.S.A.	47.4°N	163	Vm-VII	608	Douglas fir	S	1 year	2037	2709	Vogt et al. 1980
Stampede Pass/Wash.	U.S.A.	47.3°N	1150	Vm	438	fir forest	S	1 year	2277	3028	Vogt et al. 1980
Shigayama (Honshu)	Japan	36.7°N	1790	VI (sub-alpine)	463	conifers	S	1 summer	460	612	Takai et al. 1977
Virelles	Belgium	50.1°N	245	VI	609	deciduous forest	S	34 months	692	920	Froment 1972
London	England	51.2°N	45	VI	561	deciduous forest	S	1 year	2269	3017	Anderson 1973
Oxford	England	51.7°N	63	VI	613	beech forest	S	10 months	470	625	Phillipson et al. 1975
Rothamsted	England	51.8°N	129	VI	613	crops	S	June-September	1404	1867	Monteith et al. 1964
Aiken/SC	U.S.A.	33.6°N	161	VI	822	tall grass	S	2 years	1428	1899	Coleman 1973
Aiken/SC	U.S.A.	33.6°N	161	VI	865	pine forest	S	1 year	1865	2480	Reinke et al. 1981

Site	Country	Latitude	Elevation	Climate	AET	Vegetation	Measuring method	Measuring duration	Raw CO_2	Adjusted CO_2	Source
Oak Ridge/Tenn.	U.S.A.	36.0°N	305	VI	764	deciduous forest	D	1 year	3800	3800	Edwards & Sollins 1973
Oak Ridge/Tenn.	U.S.A.	36.0°N	305	VI	911	pine & deciduous forest	S	1 year	1526	2030	Witkamp 1966a 1966b
Cedar Ck./Minn.	U.S.A.	45.0°N	900	VI	576	forest fen swamp	D	1 year	2909	2909	Reiners 1968
Columbia/ /Missouri	U.S.A.	39.0°N	237	VI-VII	735	tall grass	D	22 months	1652	1652	Kucera & Kirkham 1971
Jornada/N. Mexico	U.S.A.	32°N	1350	VII-III	225	grassland	S	9 months	1102	1465	Parker et al. 1983
Pawnee Grassland/ /Colorado	U.S.A.	42.5°N	1650	VII	317	short grass	S	February-November 1972	511	680	Klein 1977
Moxee City/Wash.	U.S.A.	47.0°N	472	VIIa	203	shrub steppe with grass	S	19 months	135	180	Wildung et al. 1975
Matador/Sask.	Canada	50.8°N	680	VII	394	grass	T	3 growing seasons	1095	1095	De Jong et al. 1979
Murmansk	Russia	67.0°N	22	VIII	328	open pine woodland	?	May-July 1964-65	500	500	Repnevskaya 1967
Maurset	Norway	60.4°N	778	VIII	301	birch	D	1 summer	2530	2530	Van Cleve & Alexander 1981
Hardangervida	Norway	60.3°N	1320	VIII	165	snow valley	D	1 summer	650	650	Van Cleve & Alexander 1981
Abisko	Sweden	68.4°N	388	VIII-IX	263	alpine raised bog	D	1 summer	184	184	Svensson et al. 1980
Barrow	Alaska	71.3°N	10	IX	94	tundra	D	June-August 1973	140	140	Peterson & Billings 1975

The sites are arranged by bioclimate type according to the genetic system of Walter and Lieth (1960-67):
I = equatorial; II = tropical summer-rain; III = subtropical arid; IV = mediterranean; Ve = warm-temperate (east-coast); Vm = marine west-coast; VI = typical temperate; VII = temperate continental (VIIa = temperate semi-desert); VIII = boreal; IX = polar.
Also shown are average annual actual evapotranspiration (AET), vegetation type, and the CO_2 data. CO_2 evolution was measured by four methods (see main text), denoted here by S (static), D (dynamic), T (theoretical), and ? (not described). For the static method, all raw values were adjusted by a factor of 1.33, as suggested by Haber (1959).

also recorded for each site. This data-base is shown in Table 1 and covers almost the entire range of climates on earth. Shown in Table 1 are site location, vegetation type, bioclimatic type (Walter and Box 1976) and selected climatic data, some aspects of CO_2 measurement, raw and adjusted CO_2 evolution, and the source for the CO_2 data.

More sites are available for the northern temperate zone than for other regions, but all main world climate types are represented except subtropical deserts. A very few CO_2 measurements were excluded from the analysis due to poor site description, but most questionable situations involve severe environmental and/or measurement problems. One site in Venezuela (Medina et al. 1980), for example, involved an exceptionally nutrient-poor, podzolized sand substrate (with low CO_2 evolution), while other sites represent situations with varying degrees of poor drainage. These sites may not reflect climatic relationships with CO_2 evolution but are included in the data-base, at least initially, in order to have more complete geographical coverage and representation of the factors which may control CO_2 evolution. The environmental variables available at each site and their correlation coefficients (r) relative to annual CO_2 evolution (n = 48) are given in Table 2.

Table 2. Site environmental variables and correlation coefficients (r) versus raw and adjusted annual CO_2 evolution

Factor	Symbol	Raw CO_2 evolution	Adjusted CO_2 evolution
mean annual temperature	TY	0.37	0.45
warm-month mean temperature	TMAX	0.35	0.41
cold-month mean temperature	TMIN	0.35	0.44
mean-temperature range (TMAX-TMIN)	TRANGE	-0.26	-0.35
annual precipitation	PY	0.18	0.25
precipitation in driest month	PMIN	0.12	0.15
precipitation range (PMAX-PMIN)	PRANGE	0.14	0.22
annual potential evapotranspiration	PETY	0.35	0.43
annual moisture index (PY/PETY)	MIY	0.001	0.04
lowest monthly P/PET	MIMIN	-0.08	0.07
annual actual evapotranspiration	AETY	0.38	0.45
climatic water deficit	DEFY	-0.08	-0.06
climatic water surplus	SURPY	0.08	0.13
humidity index (SURPY/PETY)	IHY	-0.04	-0.01
aridity index (DEFY/PETY)	IAY	-0.26	-0.25
soil pH (estimated)	PH	-0.10	-0.12

INITIAL STATISTICAL ANALYSIS

As a first step in data analysis, correlations and bivariate plots were produced for all independent variables against raw and adjusted CO_2 evolution rates, in order to examine the nature of possible relationships. These results (cf Table 2) suggest that temperature and AET (actual evapotranspiration) may be the primary

controls but that secondary factors are also important in many situations. Latitude is not a climatic variable but was used by W.H. Schlesinger (1977) in one of the few existing studies of the global dimensions of soil CO_2 evolution. This study produced a good statistical fit with annual CO_2 evolution rates ($r^2 = 0.60$), but the data-base did not include aberrant tropical sites. As can be seen in Table 2, no single environmental variable has a strong statistical correlation with CO_2 evolution. Since AET combines temperature effects and simultaneous water availability in one variable, it is a useful geographic index of climatic "favourableness" and thus provides a good initial basis for examining the global behavior of climate-related processes. In order to check the global behaviour of annual CO_2 evolution, including raw versus adjusted measurement values, these data are plotted against annual AET in Figure 1. The higher values obtained by the "dynamic" measurement methods appear to suggest a trend of increasing potential CO_2 evolution with increasing annual AET. Adjustment of the CO_2 evolution values from "static" measurement methods seems to bring the higher "static" values in line with this suggested trend (corroborating W. Haber's 1.33 correction factor). The fact that many values fall well below the suggested potential, however, suggests that non-climatic factors, especially soil and topographic conditions, are important at many sites.

Possible bias of CO_2 evolution estimates by longer or shorter periods of measurement is examined in Figure 2, using the adjusted CO_2 data only. In no part of the scattergram does there seem to be any consistent difference between values from short-term versus long-term measurements, and in fact these data seem generally to coincide. Short-duration measurements can be extrapolated to annual estimates perhaps only in the aseasonal humid tropics (i.e. the data of Wanner et al. 1973), but full-year and some multi-year tropical studies gave similar, both high and anomalously low CO_2 totals.

Simple correlation-regression analysis with the initial data-base (n=34) suggested a power-function relationship between annual AET and CO_2 evolution ($r = 0.47$), of the form

$$CO_2 \text{ evol.} = 0.643\,AET^{1.2274} \qquad (1)$$

where AET is in mm/year and CO_2 is in g CO_2/m^2/year. This equation was applied to a world mapping system coupled to a large world climatic data-base (Box 1981) in order to produce a preliminary "research map" of CO_2 evolution. Such maps can be quantified by computerized planimetry (Box 1975), yielding estimates of global totals which can be compared with global estimates of other carbon-balance components. Volumetry of this map produced an estimate of 230.3×10^9 metric tons of CO_2 evolved annually by the world's land areas, which is equivalent to 125.5×10^9 t dry matter (1g C = 2.0 g dry matter). These values are about the same as estimates of world terrestrial net primary productivity based on the same mapping system and climatic data (Box 1975, 1978), which range from about 105 to 125×10^9 t dry matter/year. This result with the

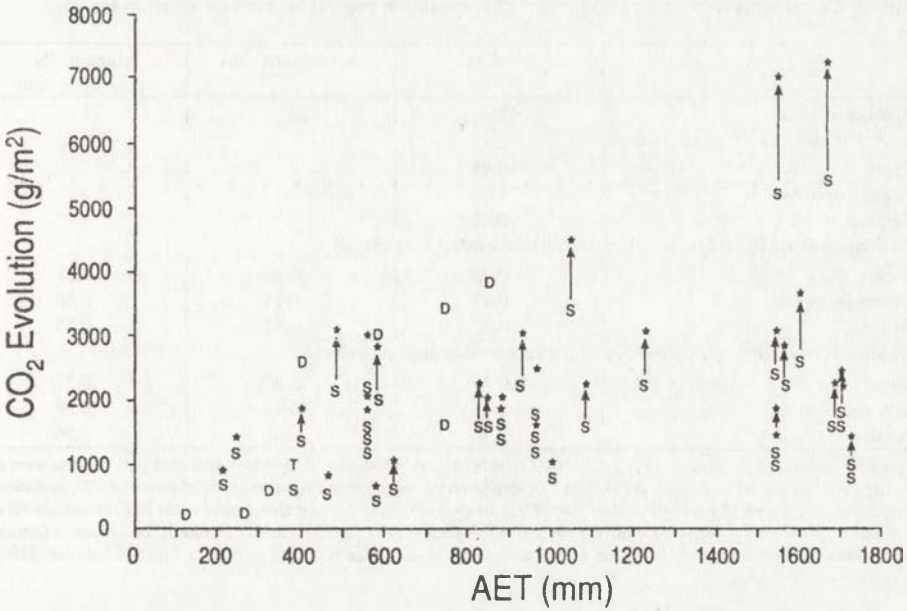


Fig. 1. Raw and adjusted values of measured annual soil CO_2 evolution from various biomes and topographic-edaphic situations worldwide plotted against annual actual evapotranspiration (AET)

The measurement method (see main text) is indicated for the particular site values as follows:
S = static method (raw); * = adjusted static method; D = dynamic method (not adjusted); T = theoretical method (not adjusted).
The dynamic values and highest adjusted static values together suggest a trend of increasing CO_2 evolution with AET, but with numerous aberrations.

earlier data-base, however, does not treat the question of possibly quite low CO_2 evolution values over larger tropical areas. This initial estimate of annual terrestrial CO_2 evolution was presented (Box et al. 1983) but does not represent a geographically reliable world model and was not published.

The full data-base (n=48) was used for all subsequent analyses. The data for adjusted annual CO_2 evolution are plotted in Figure 3 against annual AET, with symbolism representing the respective vegetation/landscape types. This type of scattergram yields a more geographic overview of the behaviour of a geographically varying phenomenon. The data plot in Figure 3 shows large deviations throughout. In the 500-800 mm AET range, measured CO_2 evolution has nearly a four-fold range. The birch forest at Hardangervidda (see Table 1), for example, has CO_2 evolution much higher than might be expected. This could be the result of infrequent sampling at this site and the use of a suction device to sample the soil atmosphere. In the humid tropics, many sites show CO_2 evolution values far lower than expected.

The full data-base was analyzed by correlation-regression procedures, including tests for linear, saturation-curve, and sigmoid relationships between adjusted CO_2 evolution and environmental factors, especially AET. Due mainly to the aberrant tropical sites, however, all correlation coefficients were low, with little difference between different curve shapes (see top part of Table 3).

Table 3. Correlation coefficients (r) for soil CO_2 evolution models without an aeration factor

	all sites	unsaturated sites	climatically controlled sites
Number of sites	48	30	37
(a) Regressions based on all 48 sites			
linear	0.45	-	-
saturation-curve	0.46	-	-
sigmoid	0.42	-	-
(b) Statistical models (regressions) based on unsaturated sites (n=30)			
linear	0.45	0.80	0.57
saturation-curve	0.47	0.76	0.58
sigmoid	0.42	0.83	0.55
(c) Models of climatic potential CO_2 evolution based on highest values			
linear	0.45	0.80	0.57
saturation-curve	0.48	0.73	0.58
sigmoid	0.44	0.81	0.56

Regression models were attempted for all sites (n=48) and for subset (n=30) involving only unsaturated sites. Models were also produced by fitting a curve through the highest CO_2-evolution values, representing an estimate of potential CO_2 evolution at the well aerated, climatically controlled sites (n=30). The models of (b) and (c) were also applied to the full data-set (n=48) and to a subset (n=37) involving only climatically controlled sites (i.e. excluding unusual topogenic or edaphic situations). Correlation coefficients are highest for the unsaturated, better aerated sites but show very little variation between different curve shapes or positions.

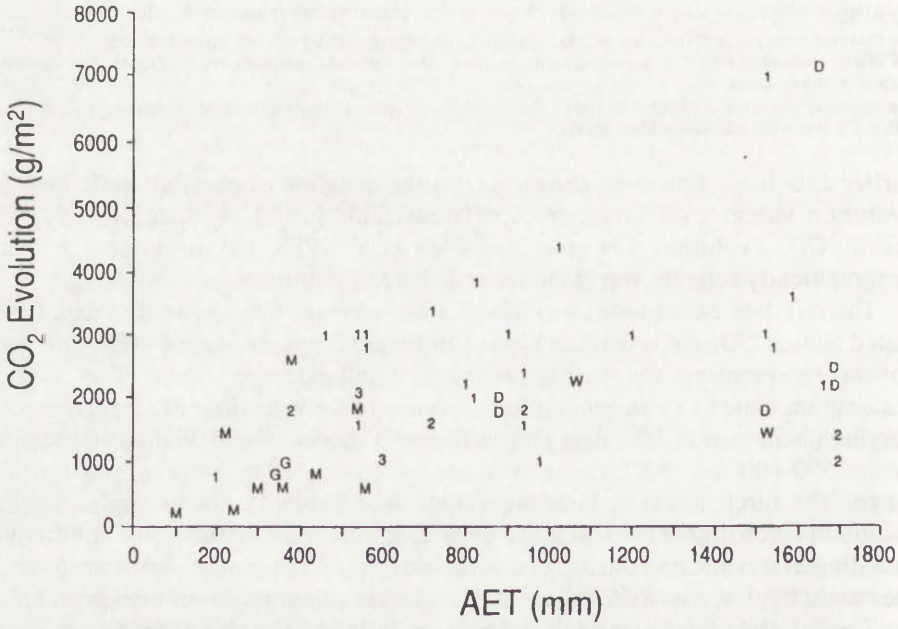


Fig. 2. Adjusted annual CO_2 evolution data and measurement duration (plotted against annual AET)

The duration of CO_2-evolution measurements is indicated as follows:
1, 2, 3 = no. of complete years of measurement; G = complete growing season; M = several months (less than complete year or growing season); W = few weeks (generally about 2, only tropical); D = few days (3-10, only in tropical Asia). There does not appear to be any systematic difference between values from short-term versus long-term measurements.

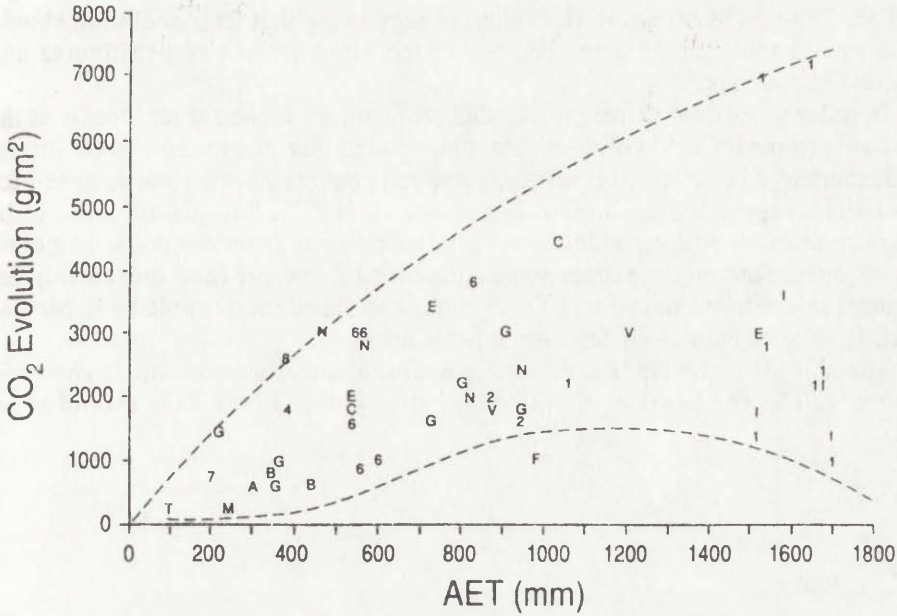


Fig.3. Adjusted annual CO_2 evolution for landscapes worldwide, plotted against annual AET

The landscapes involved are indicated by the following symbolism (numbers from Walter climatic affinities):
1 = tropical rainforest; I = tropical "heath" forest, etc.; 2 = tropical deciduous forest; F = tropical cloud forest; 4 = mediterranean scrub; E = evergreen broad-leaved forest (including tropical montane); 6 = temperate deciduous forest; 7 = temperate semi-desert; N = needle-leaved evergreen forest (non-boreal); 8 = boreal birch woods; B = boreal needle-leaved forest; M = mixed forest; V = tropical savanna; T = tundra; G = grassland (mainly temperate); C = cropland; A = alpine vegetation.
CO_2 evolution seems to increase with increasing warmth and wetness (AET), but many sites fall below this suggested potential (upper dashed curve), especially the group of equatorial forests at AET 1400 mm. Various grassland (G, V), deciduous forests (2, 6), and some conifer forests (N, B) also fall well below the suggested potential. The lower dashed line represents only the apparent general lower limit of CO_2 evolution. Only the perhumid tropical cloud forest (F) at AET=977 mm falls below this line.

CO_2 EVOLUTION AND SOIL FACTORS

Procedural problems in measuring CO_2 evolution are legendary, so it is likely that some of the remaining unaccounted variance is error variance. Also, it was not possible to include short-term wetting and drying phenomena in this study or to relate CO_2 evolution to measured site productivity or adequate soil descriptions. Tight clay soils, for example, could restrict CO_2 diffusion (Schlesinger 1977). The most striking suggestion from Figures 1-3, however, is that of a major divergence of CO_2 evolution in warmer, wetter climates, especially the humid tropics. This "tropical question" in attempts to find global relationships between biosphere processes and environmental factors is not new but was also seen in some data for primary production, decomposition rate, and other processes. Soil types, soil nutrient status, and other factors may vary more widely and become more patchy in the tropics, confounding simple climatic relationships. E. Medina

and M. Zelwer (1972) quote H. Walter as suggesting that CO_2 evolution should be lower in the equatorial region, due to the rapid actions of detritivores and nutrient scavengers.

In order to gain some insight into this problem, we looked more closely at the available tropical CO_2-evolution data, upon which this study seems to be strongly dependent. Unfortunately, soil type and nutrient status were not reported for most sites, especially those of H. Wanner et al. (1973). Soil pH appeared to be the only relevant soil variable for which data or even estimates could be gotten for all sites. One might expect some influence of low pH (and presumably associated low nutrient status) on CO2 evolution, as stated for example by E. Medina et al. (1980) for their low-CO_2 sites at San Carlos.

The soil pH (estimated) at each CO_2 evolution measurement site is shown in Figure 4. The scattergram shows some indication of lower CO_2 evolution on

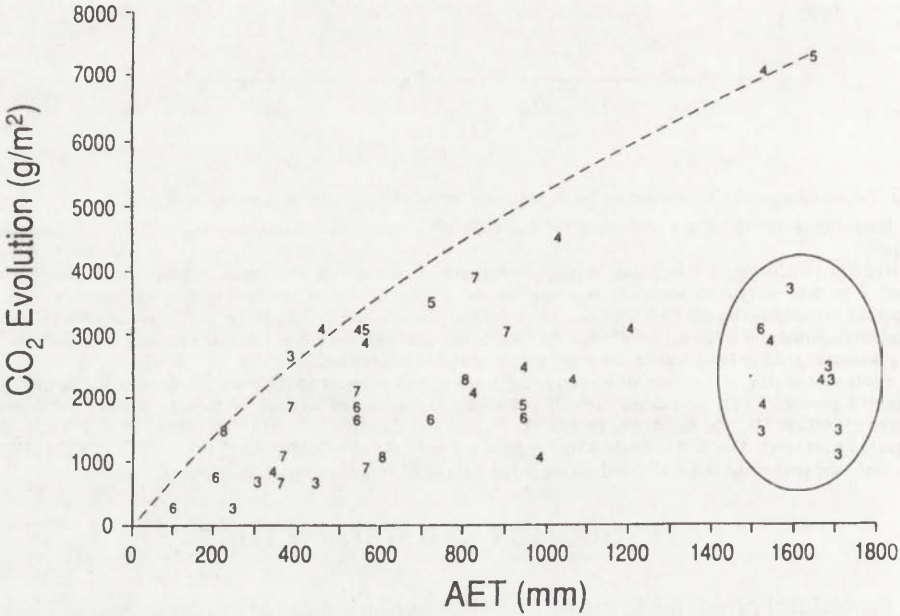


Fig. 4. Estimated soil pH and annual CO_2 evolution

Annual adjusted CO_2 evolution is plotted against annual AET, with soil pH estimates shown for the individual measurement sites. The hand-drawn curve represents the suggested climatic potential CO_2 evolution, with many sites falling below this line, perhaps due to unusual substrate conditions which retard CO_2 evolution. Most of the equatorial forest sites (circled) show low pH values, but one is high and these values are not conclusively lower than the soil pH values of the two rainforest sites which have much higher CO_2 evolution (on the curve).

more acidic soils, but the pattern is not consistent. In particular, the low equatorial sites (circled) do not have soil pH values drastically lower than those of the two equatorial sites with high CO_2 evolution.

A similar comparison was made using the difference between estimated soil pH and that expected by a climate-based, global soil-pH trend curve. There was a

somewhat stronger suggestion of low CO_2 evolution from more acidic soils, but such pH "data" and trends are too speculative for model construction.

An attempt to represent the low nutrient status of tropical soils was also made by means of a climate-based index of potential leaching. This leaching index did show some relationship to CO_2 evolution but cannot differentiate high and low CO_2 evolution rates for sites with roughly the same climate. Further statistical analyses using soil pH or the leaching index were not performed.

If one looks closely at Figure 3, one sees not only that the scatter becomes much greater in the humid equatorial region, but also that some CO_2 values actually appear to decrease with greater AET. As a result, the relationship between annual CO_2 evolution measurements and annual water balance, as expressed by the annual moisture index (MI), was plotted as shown in Figure 5. The equatorial forest sites with very low CO_2 evolution have MI values above 2.0 (except one site), whereas the two tropical rainforest sites with higher CO_2 evolution have not such high total rainfall and may thus have better soil aeration. Some extratropical sites are also very wet (MI > 1.0), but most of these are in mountains, with perhaps better drainage.

Not only the total rainfall but also its seasonality may be important. Annual CO_2 evolution is plotted against the lowest average monthly precipitation amount

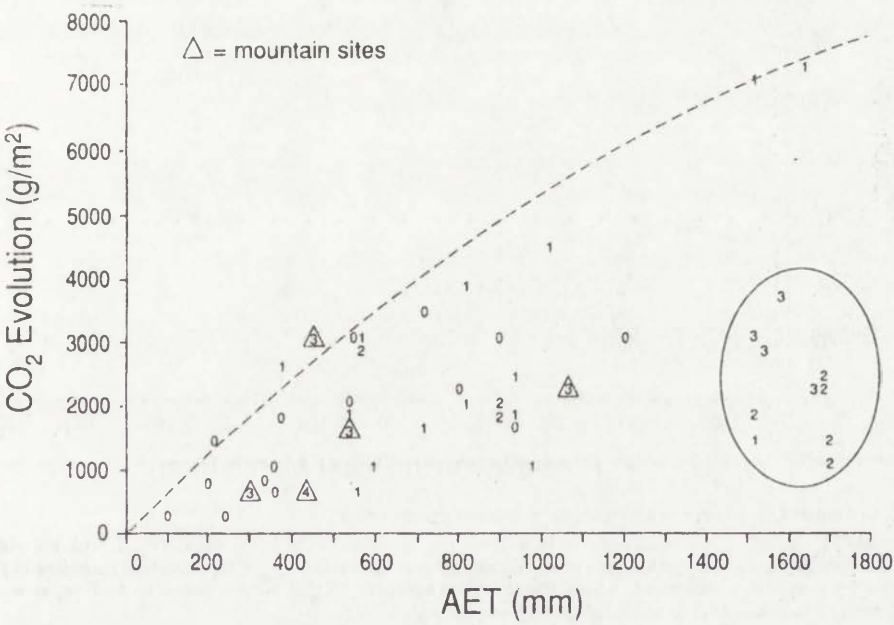


Fig. 5. Annual CO_2 evolution and annual water balance

Annual CO_2 evolution is plotted against annual AET, as in Figure 4, but with individual sites shown by the integer portion of their moisture index (MI, precipitation divided by PET). Mountain sites often are wetter and are indicated by triangles. The anomalous equatorial forest sites (circled), with low CO_2 evolution, all have MI values above 1.33, whereas the two rainforest sites with higher CO_2 evolution (on the curve) have MI values of only 1.30 and 1.34.

(P_{min}) in Figure 6. In this data-base only tropical forest sites have more than 90 mm of precipitation in their driest months, and for these sites there is a clear suggestion of decreasing CO_2 evolution with the disappearance of a drier season sometime during the year. This can be interpreted as increasing soil saturation and poor soil aeration. The two tropical rainforest sites with high CO_2 evolution, on the other hand, have less precipitation (59 and 80 mm) in their driest months, and less total precipitation (cf. Figure 5).

Soil aeration may be a major factor controlling soil CO_2 evolution, perhaps especially in the humid tropics. Thus, statistical analyses were repeated for a data-subset (n=30) involving only those sites which did not appear to have saturated soil (climatic or topogenic) or saturated atmospheric conditions (i.e. the tropical cloud forest). Correlation coefficients increased to around r = 0.80 for these sites (n=30) and yielded regression equations which seem more acceptable from a modeling perspective. (When applied to the full data-base, of course, the r-values are no better than before, only the curves climb to higher CO_2 evolution levels.)

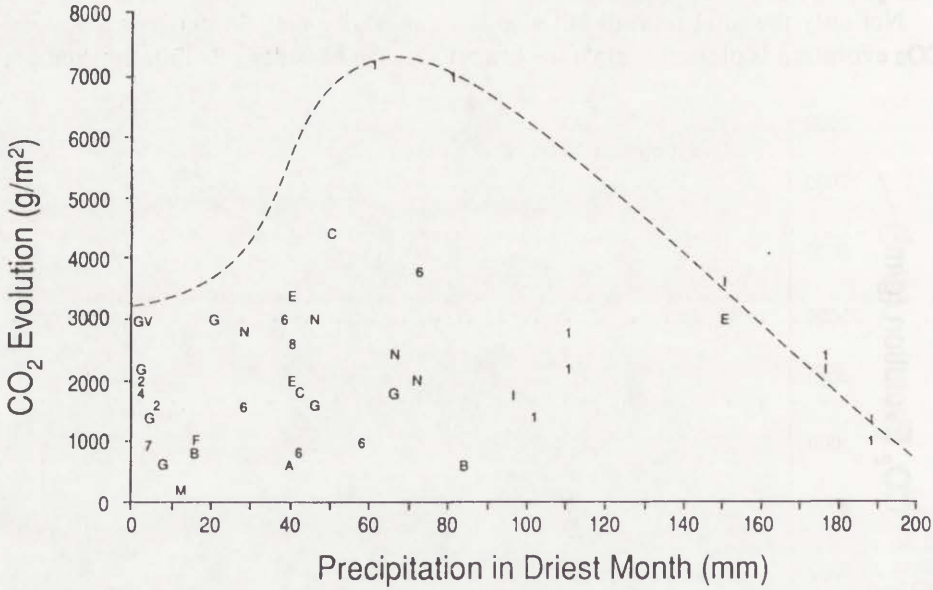


Fig. 6. Annual CO_2 evolution and seasonal minimum precipitation

Annual CO_2 evolution is plotted against the average precipitation in the driest month (P_{min}), with individual sites shown by landscape symbolism (as in Figure 3). With increasing P_{min}, CO_2 evolution increases at first as the dry season is ameliorated. Above about 60 mm however, CO_2 evolution seems to decline, as wetter and wetter conditions lead to saturated, poorly aerated soil.

Finally, these regressions were also performed on a data-subset involving only those sites (n=37) which can be considered to be under climatic control. This includes all unsaturated sites (n=30) plus some moderately saturated sites,

but excludes sites strongly influenced by topography and/or very nutrient-poor soil. These regressions for climatically controlled sites yield r-values around r = 0.57; results are summarized in part (b) of Table 3.

POTENTIAL CO_2 EVOLUTION

With this potential explanation for the low CO_2 evolution values in ever-wet tropical forests, one can now see the suggestion of a linear, or possibly saturation or sigmoid, relationship between climatic potential CO_2 evolution and AET at the remaining, climatically controlled sites (cf. Fig. 3 or 5). A final model might take the form of some function of annual AET, modified by the effect of aeration. With a theoretical basis and hypothetical mathematical form provided, relatively few data are needed for parameterization, primarily those for end-points and general curvature. Thus, in addition to statistics-based models, models for climatic potential CO_2 evolution were produced by fitting curves are fit directly through the origin and the highest CO_2 evolution values, in particular the maximum value, 7212 g CO_2/m^2/year at the Khao Chong Forest Reserve in Thailand (Yoda and Kira 1969), which also has the highest AET value, at 1644 mm. This apparent heresy is justified by the fact that the lower CO_2 values in the wide scatter do not represent potential CO_2 evolution. A linear model through this highest CO_2 value has the form

$$CO_2 = m \cdot AET \tag{2}$$

where m = 7212/1644. Such a straight line from the origin to the highest CO_2 point would be exceeded by some site data, suggesting a slight saturation effect. A saturation curve fit through this same extreme value and with an asymptote of 9 kg CO_2/m^2 (based on statistical trials) has the form

$$CO_2 = 9000\left[1 - e^{-\alpha \cdot AET}\right] \tag{3}$$

where α = 1/1644 $\log_e$ (1- 7212/9000). A sigmoid model was fit similarly through the highest CO_2 value, with inflection at AET = 1000 mm/year and the same asymptote, and has the form

$$CO_2 = \frac{9000}{1 + e^{\alpha - \beta \cdot AET}} \tag{4}$$

where α = [1/(1-1644/1000)] $\log_e$ [(9000/7212) - 1] and $\beta = \alpha / 1000$

Correlations were next run between measured CO_2 evolution and that predicted by equations (2-4), for the full data-set (n=48) and the subsets for unsaturated sites (n=30) and climatically controlled sites (n=37). These results are shown in part (c) of Table 3. The residuals (n=48) between measured CO_2 evolu-

tion and that estimated by equations (2-4) were also plotted (not shown), separately with symbolisms for soil pH, total wetness (MI), and the landscape type. There was no consistent relationship between soil pH and model residuals, but negative residuals (i.e. lower CO_2 evolution than expected) became greater as MI increased beyond about 1.5.

SOIL AERATION AND A FINAL MODEL

Equations (2-4) represent models for climatic potential CO_2 evolution. In order to represent the effect of soil aeration, an aeration index (aer) was developed, expressed by

$$aer = e^{-\alpha (MI_{min} - 0.6)} \quad \text{(but never} > 1.0) \qquad (5)$$

where MI_{min} is the moisture index of the driest month, and is such that aer = 0.5 at MI_{min} = 0.6 (based on the CO_2 evolution data). This artificial index represents the hypothesis that the soil has a sufficient period for aeration and CO_2 evolution if $MI_{min} < 0.6$, but that aeration decreases toward permanently saturated conditions, with consequent re-duction of CO_2 evolution, as MI_{min} increases beyond 0.6. In reality, MI_{min} only represents precipitation, and much water may remain in the soil during periods when the monthly MI is not far below one. The cloud forest at Rancho Grande (Vene-zuela) was given the value aer = 0.25 and the raised bog at Abisko (northern Sweden) the value aer = 0.125, based on their measured versus expected CO_2 evolution. (This logic is somewhat circular but does permit reasonable geographic extrapolation to similar sites elsewhere.)

The utility of this aeration index can be seen in Figure 7, in which residuals of the linear CO_2 model (equation 2) are plotted against Pmin, with symbolism representing tenths of the value of the aeration index (equation 5). The plot suggests a threshold effect, by which CO_2 evolution is re-tarded by poor soil aeration for driest-month pre-cipitation levels above about 80 mm. This is interpreted as the lack of any drier season during which accumulated soil organic matter might decompose and release CO_2.

Given the apparent relationship to soil aeration, final global models for annual CO_2 evolution may take the form

$$CO_2 \text{ evol.} = f(AET) - X(1 - aer) \cdot f(AET)]$$

where f(AET) is a model for soil CO_2 evolution (i.e. equations 2-4), aer is the aeration index, and X is a coefficient for the strength of the soil-aeration effect on CO_2. This coefficient X is calculated so that the resulting estimate of CO_2 evolution will coincide with the lowest measured CO_2 evolution among the high-AET (equatorial) sites. Using the extremely low CO_2 evolution of 1002 g/m^2 on plinthitic laterite at San Carlos de Rio Negro (Medina et al. 1980), X would have

a value of roughly 1.40 for all three curve shapes. Global models for annual CO_2 evolution derived from the above assumptions and procedure would thus have the form

$$CO_2 \text{ evol.} = \hat{CO}_2 - 1.4\left[(1 - \text{aer})\,\hat{CO}_2\right] \qquad (6)$$

where aer is from equation (5) and $\hat{CO}_2$ from any model for climatic potential CO_2 evolution (e.g. equations 2-4).

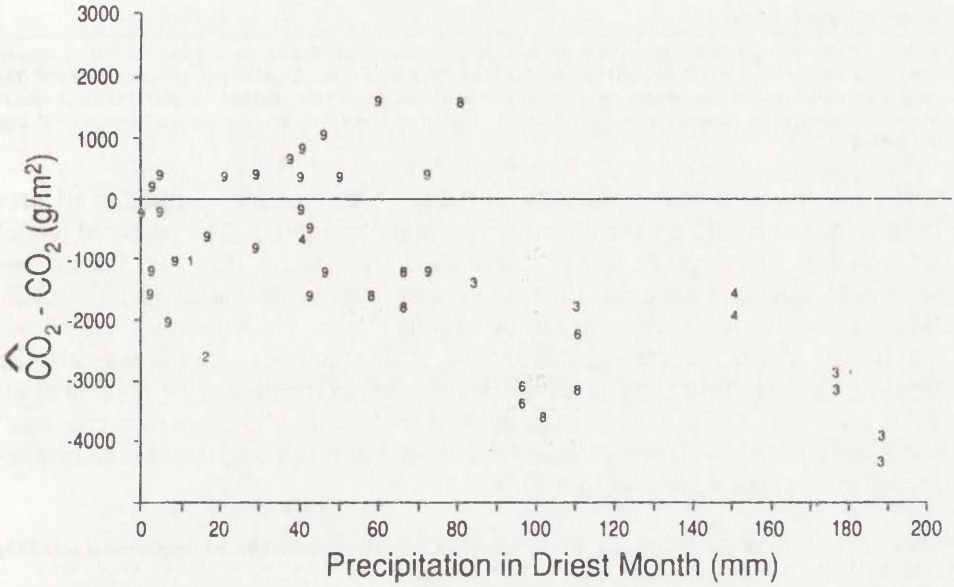


Fig. 7. Residuals of a model of potential CO_2 evolution, as related to poor soil aeration

The residuals represent measured CO_2 evolution minus the potential CO_2 evolution predicted by the saturation-curve model of equation (3) (i.e. retarded CO_2 evolution falls below the horizontal line). Individual sites are indicated by values of the soil aeration index (tenths), as calculated using equation 5 in the main text. Soil CO_2 evolution becomes lower and lower, below otherwise expected levels, as P_{min} increases and soil aeration values fall below 8 tenths.

FINAL RESULTS

The above aeration correction was applied to the previously derived statistical equations (part b of Table 3) and equations (2-4) for potential CO_2 evolution (part c of Table 3), and correlation coefficients (r) and residuals were calculated. The effect of the aeration correction on the linear CO_2 evolution models is shown in Table 4. The aeration factor alone improves r from 0.45 to 0.69 for both linear models when they are applied to the full data-base (n=48).

Table 4. Correlation coefficients (r) for linear soil CO_2 evolution models without and with an aeration factor

	No aeration	Models with aeration factor		
	all sites (n=48)	all sites (n=48)	climatic sites (n=37)	climatic sites questionable CO_2 deleted (n=35)
Statistical model based on unsaturated sites	0.45	0.69	0.71	0.80
Model for potential CO_2 based on highest values	0.45	0.69	0.71	0.80

Both models show much better results with an aeration correction added. Results are improved further if unusual topographic-edaphic situations (11 sites) and questionable, older CO_2 measurements (2 sites — perhaps more) are deleted. The correlation coefficients of the two models are identical (as are almost all those for the other curve shapes). The distribution of residuals, however, varies dramatically (see Table 5). Ariuau and Oxford were deleted from the "climatic" subset with 35 sites (see Table 6).

The distribution of the residuals for the two linear models, applied to all sites (n=48), however, differs considerably, as shown in Table 5. The potential model (cf. equation 6) overpredicts many more sites, some badly, than does the statistical model, but these are often sites with unusual topogenic and/or edaphic conditions. Even the data sub-set for unsaturated sites (n=30), however, shows significant scatter, suggesting that factors other than poor aeration may also be limiting CO_2 evolution (e.g. poor nutrient status, as mentioned by Medina et al. 1980 for white, podzolized sand at an Amazonian site with "Amazon caatinga" scrub vegetation). Deletion of non-climatic sites and two questionable CO_2 measurements increases r further to 0.80 (n=35).

Table 5. Residuals of the "statistical" linear model and the linear model based on potential soil CO_2 evolution, with aeration correction

	Total	< 20%	20-50%	50-100%	> 100%
Statistical linear model	48				
overpredicted	25	5	9	6	5
underpredicted	23	4	19	0	0
Scaled potential model	48				
overpredicted	31	6	4	11	10
underpredicted	17	11	6	0	0

The numbers represent sites over- or underpredicted in the full data-base (n=48) used to develop the model., based on standardized residuals of the form:

$$\Delta = (C\hat{O}_2 - CO_2) / CO_2$$

The "statistical" model splits the datum-cloud fairly evenly, while the model based on potential CO_2 overestimates more sites (many of which, unusual microclimatic, soil, or topogen situations). Both models show the same correlation coefficient (r=0.69 for all 48 sites, see Table 4).

Those sites which show consistently large residuals for all or most model forms are listed in Table 6. Of these, Ariuau (Brazilian Amazon) and Oxford (U.K.) are the most problematic, but both involve relatively older measurements and values which could not be completely understood from the original papers.

Of the remaining 11 sites, about half represent unusual substrates (e.g. gley, organic soil, plinthite), topogenic situations (e.g. strand, alluvial), or vegetation (e.g. secondary grassland in a forest climate).

Table 6. Largest residuals of (linear) models for soil CO_2 evolution, with aeration factor

Site	AET	Soil	Vegetation	Measured CO_2	Standardized "statistical" model	Residuals model for "potential" CO_2
Ariuau (Brazil)	1517	latosol	rainforest	1410	-2.06	-2.91
Oxford (England)	551	thin/lime	deciduous forest	758	-1.49	-2.19
Pangandaran	1524	gley	strand forest	1710	-1.16	-1.76
Gunung Mulu	1662	podzol/gley	alluvial forest	2167	-1.14	-1.74
Chakia (Varanasi)	933	?	raingreen forest	1561	-1.05	-1.62
San Carlos/Rio Negro	1696	plinthite	rainforest	1002	-0.93	-1.46
Pawnee (Colorado)	369	sandy loam	short grass	680	-0.86	-1.38
Virelles	598	rendzina	deciduous forest	920	-0.86	-1.37
Panganduran	1524	latosol	rainforest	2136	-0.73	-1.21
Baluran	876	?	savanna	1883	-0.60	-1.04
Point Barrow	101	organic	tundra	230	-0.50	-0.92
Columbia (Missouri)	722	loess/till	tall grass	1652	-0.50	-0.92
Aiken (S.Carolina)	949	sandy clay	2° grass	1899	-0.48	-0.89

Standardized residuals (see legend of Table 5) are shown for the linear "statistical" model and for the potential-based linear model for soil CO_2 evolution, both with the aeration correction. The residuals of the potential-based model are greater (at the high end of the scale only), but most represent unusual situations and/or questionable CO_2 measurements.

MODEL RESULTS AND MORE RECENT MEASUREMENTS

Since the original CO_2 data-base was compiled (1983), measurements of CO_2 evolution have continued, with improved techniques. One major advance involves analysis of soil efflux by infra-red gas analysis or chromatography, without air pumps or chemical operations. Other improvements involve the use of NaOH instead of KOH in the "static" method (requiring no adjustment of raw values, see Nakane et al. 1983) and the use of hybrid, combination methodologies (e.g. Dörr and Münnich 1987).

Although there was no exhaustive search for validation sites, various newer CO_2-evolution studies had been collected since 1983 and provided the basis for a validation data-base. From these studies, all those newer studies which readily yielded annual, understandable estimates of CO_2 evolution were kept for validation of the above models. No studies which could be readily understood were excluded. This procedure yielded 10 validation sites, ranging from the equatorial to subarctic, including additional results from some regions in the original data-base. The climates for these 10 validation sites were estimated, water balances were run, and CO_2 evolution was calculated from the final model (equation 6). One of these sites

Table 7. Measured and estimated annual CO_2 evolution at validation sites, plus site environmental data

	Elevation (m)	Climate	AET (mm)	P_{min} (mm)	Soil	Vegetation	Method	Measured (g CO_2/m^2)	Calculated (g CO_2/m^2)	Data & Source
Barro Colorado Island	80	I	1423	9	oxisol/alfisol	moist forest	A	5300	6410	Kursar 1989
Lake Eacham/N.Qld.	800	II-I	1051	22	red clayey	moist forest	Z	5134	4612	Maggs & Hewett 1990
Lansdown res. Stn./Qld.	50	II	852	7	sandy clay	Eucalyptus woods	A	3800	3738	Holt et al. 1990
Naini Tal/N. India	2050	II	856	7	limestone	Quercus-conifer	S	4417	3772	Tewary et al. 1982
Fuchu/Japan	300	Ve	873	47	sandy loam	pine forest (2°)	Z	4767	3638	Nakane et al. 1983
Bradford Co./Florida	60	Ve	1206	48	humic sand	pine plantation	Z	4767	5292	Ewel et al. 1987
Ashland Wildlife/Missouri	200	VI	712	48	loess/limestone	Quercus-Carya	D	3715	3125	Garrett & Cox 1973
Heidelberg/ /Germany	120	VI	605	42	loamy/sandy	grass/Fagus forest	H	2310	2480	Dörr & Münnich 1987
Schefferville/ /Quebec	490	VIII	356	23	peat	sedge fen (wetland)	S	638	1109	Moore 1986
Bonanza Creek/Alaska	130	VIII	291	6	loess	Picea glauca	Z	1536	1277	Gordon et al. 1987

Soil CO_2 is estimated by the linear hand-fit model (potential CO_2 evolution) with aeration factor, as described in the main text (equation 9). Measurement methods are as before
(S = alkali "static" method, D = "dynamic" pump method) with the addition of the following new methods and/or variants:
A = atmospheric sampling (from inside a chamber placed over the soil), analyzed by infra-red gas analysis, chromatography, etc. (no adjustment of raw values);
Z = alkali method but using NaOH instead of KOH (no adjustment of raw values, cf. Nakane et al. 1983);
H = hybrid methodology involving more than one method (usually improvements on earlier "static" method, often with IRGA or other non-chemical analysis — no adjustment of raw values).
Raw CO_2 values were adjusted only for the classic "static" method (sites Naini Tal and Schefferville).

(Schefferville) is a sedge-fen wetland, but the other nine sites can be considered unsaturated and not controlled by topography or unusual substrate. These sites, with the calculated and measured annual CO_2 evolution, are shown in Table 7.

Scattergrams and correlation analyses, as described above, were re-run with the validation data, for the linear, saturation-curve, and sigmoid "final" models (i.e equation 6). These results are summarized in Table 8. The very high correlation coefficients may be influenced partly by the smaller size of the validation data-base. Nevertheless, these results suggest that the models are relatively good for unsaturated, climatically controlled sites. The results suggest further that the newer CO_2 measurement methods may be more accurate, since none of the residuals (Table 7) is greater than 25% of the actual value, except for the wetland site.

Table 8. Correlation coefficients (r) of the potential-based models for soil CO_2 evolution (with aeration factors), for both the development and validation data-bases

	Model development		Model validation
	all sites	valid sites & CO_2	all sites
	(n=48)	(n=35)	(n=10)
linear	0.69	0.80	0.92
saturation	0.66	0.73	0.96
sigmoid	0.67	0.79	0.90

The three models are from equation (8), with linear, saturation-curve and sigmoid forms. Such models represent estimates of climatic potential soil CO_2 evolution modified by the degree of soil aeration. The data-set with 35 sites excludes 13 sites with obvious soil problems (wetlands, very low nutrient status, etc.) and/or questionable CO_2 measurements, as explained in the main text. The even better results with the validation data than with the original data supports the logic and calibration of these models.

The models for climatic potential CO_2 evolution (i.e. equation 6, cf Table 8) seem preferable to the purely statistical models, since the models for CO_2 potential represent a clearer theoretical basis, i.e. a potential CO_2 flux modified (decreased) by inhibiting soil factors. In choosing among the three curve forms, though, the correlation coefficients are less important than the balance between positive and negative residuals and between large and small residuals. For the validation sites (Table 8), for example, the saturation curve has the highest r-value but may be the worst model for those 10 sites, since all 10 sites were overestimated, one by almost 200% (though small in absolute measure). The best model appears to be the linear form (cf Tables 5-6) since it is simplest in concept, has high r-values, and for normal sites has balanced residuals and no unusually large (unexplainable) residuals in any particular biome. Residuals of this model are shown graphically in Figure 8, with landscape symbolism. The final model for global soil CO_2 evolution is thus given by equation (6), with CO_2 from the linear model of equation (2).

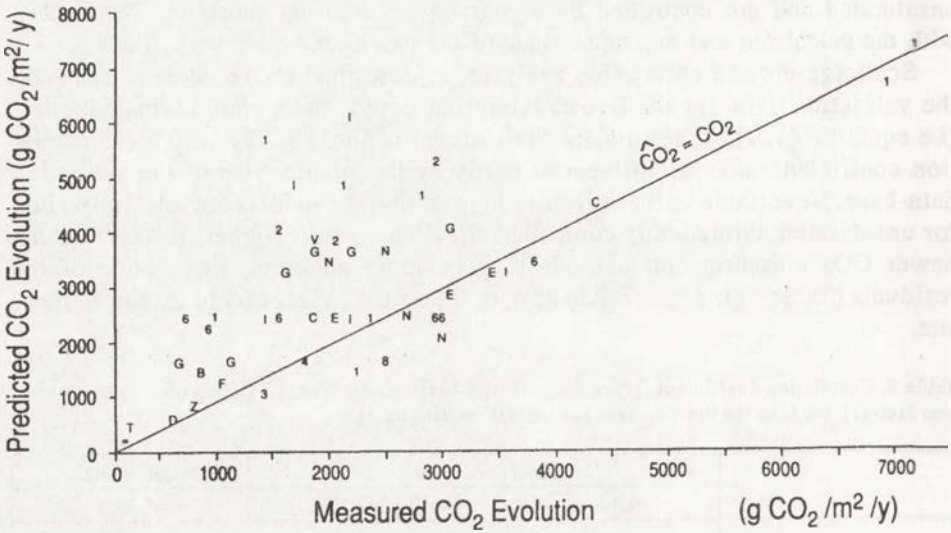


Fig. 8. Residuals of the "Final" potential-based model for soil CO_2— evolution

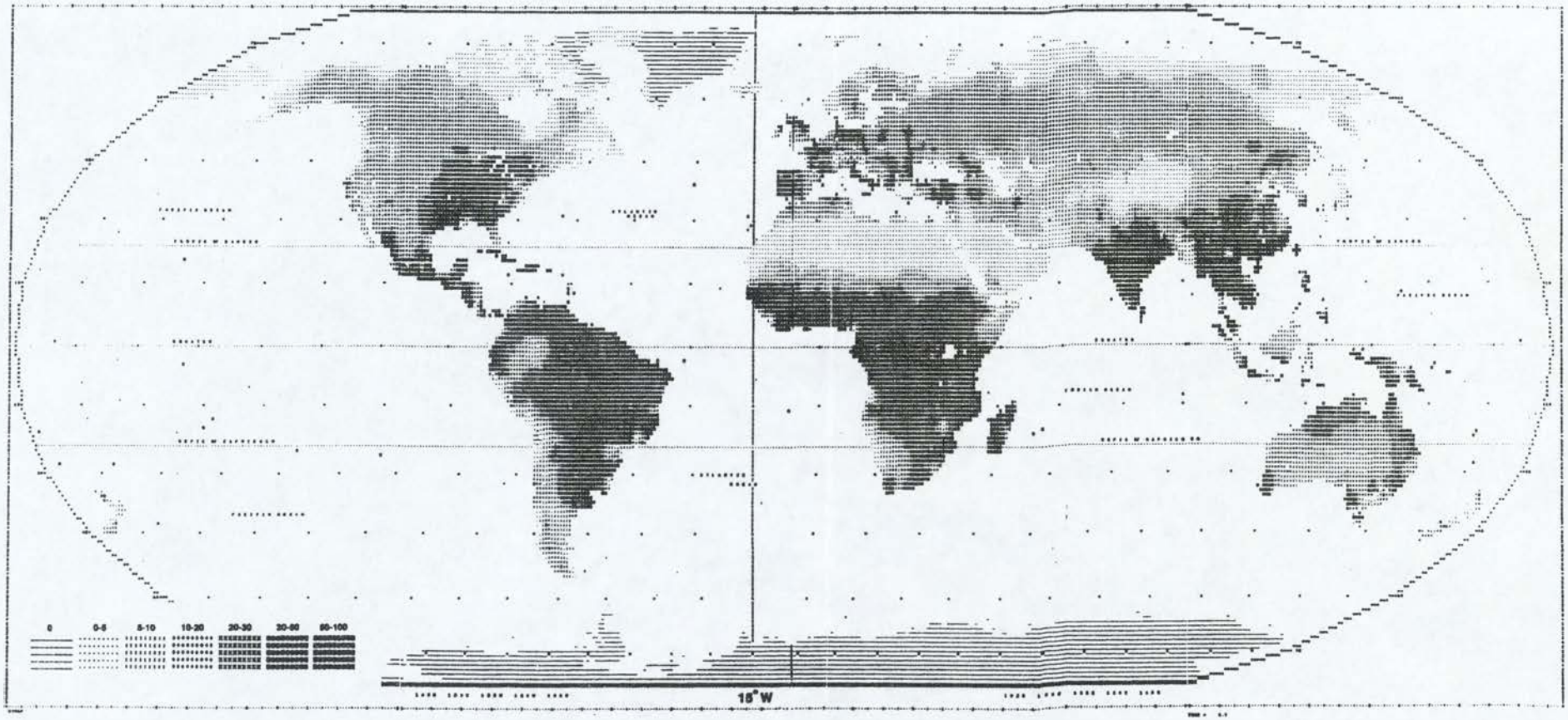
Predicted CO_2 evolution (equation 8, linear form), with aeration correction, is plotted (vertically) against measured CO_2 evolution (horizontally), for all 48 sites (with biome symbolism, see Figure 3). Overpredictions (above the diagonal line) are more numerous than underpredictions, but this results mainly from the 11 sites at which CO_2 evolution is retarded by topographic or edaphic factors (cf. Table 6)

WORLD PATTERNS

In order to estimate the global terrestrial soil CO_2 flux to the atmosphere, world maps were produced by applying the linear, saturation-curve, and sigmoid models for potential CO_2 evolution (equations 2-4), with aeration correction (i.e. equation 6), to a world climatic data-base of 1600 sites, as has been done for other geoecological predictive models (e.g. Box 1978, Brook et al. 1983, Lieth and Box 1972, 1977; Meentemeyer et al. 1982). AET and other water-balance values for these 1600 climatic sites were calculated by SOLWAT (Box 1982). The linear model identified as "best" in the previous section still appears to be the best when mapped globally, since its few larger residuals do not cover large areas.

Fig. 9. Estimated annual soil CO_2 evolution, based on climatic potential CO_2 evolution and a soil-aeration factor

The potential-based model for CO_2 evolution, with the aeration correction (i.e. equation 8, linear form), was applied to a global climatic data-base involving 1600 sites. Soil CO_2 evolution is generally expected to be high in the humid tropics but is lower in certain very wet areas which have no dry season at all (e.g. western Amazonia, Borneo). These areas may be dramatically lower but are also relatively small and have little effect on estimates of global total CO_2 evolution.



This world map, representing climatic potential annual soil CO_2 evolution modified by soil aeration, is shown in Figure 9. It shows highest evolution rates in the humid tropics and low values in both desert and polar environments, where dryness and cold, respectively, limit both biomass production and decomposer activity. The zero-intercept of the model correctly depicts low rates across the large areas of polar and arid environments on earth. The effect of poor soil aeration is evident in the wettest tropical areas (especially Borneo and western Amazonia). These regions, however, represent relatively small areas and will not greatly affect estimates of global total even if model estimates are most tenuous here.

The map for soil CO_2 evolution is similar to a climate-based map of average soil CO_2 content (log pCO_2) produced by Brook et al. (1983). It is also similar to climate-based maps of predicted primary production produced by H. Lieth and E.O. Box (1972, 1977) and appears to represent the "throughput" geographic pattern of E.O. Box and V. Meentemeyer (1991).

The global total annual CO_2 evolution represented by Figure 9 is about 275×10^9 mt CO_2 (approximately 75×10^9 mtC or about 150×10^9 mt dry matter). This is larger than our earlier estimate of about 230×10^9 mt dry matter, but this is due probably to the linear rather than power-function curve form. It also exceeds many estimates of annual terrestrial net primary production (e.g. about 125×10^9mt dry matter). Since respiration by living roots, as well as metabolism of mycorrhizal fungi, can make important contributions to measured soil CO_2 evolution, direct comparisons with metabolic activity in soil and litter are difficult. CO_2 from strictly physical processes cannot be entirely excluded; nevertheless, most of the CO_2 must come from decomposition of dead biomass.

It is also interesting to compare the form of this relationship with other AET-based models. G.A. Brook et al. (1983) produced a world model of the CO_2 content of the soil atmosphere, which takes the form of a saturation curve, relative to AET. H. Lieth and E.O. Box (1972) found a saturation-curve relationship between annual net primary production (NPP) and AET, with an upper asymptote at 3000 g dry matter per square metre per year. Litter decomposition rates worldwide generally show a linear relationship between annual percentage weight loss and annual AET (Dyer 1986), but there is much scatter of the observations from the tropics. These results for litter decay mirror our results for CO_2 evolution; observations at tropical sites appear to be greatly controlled by local aeration and the effects of nutrient status. Indeed the very diversity in species composition seems to be matched by site diversity in carbon balance dynamics.

The strong relationship between our model and the measured values in the validation data set, observations recently conducted, suggests that measurement procedures are becoming more standardized. It suggests a stronger relationship with climate than shown by the earlier observations. Many errors persist, however, and need to be corrected or adjusted. Soil CO_2 evolution also needs to be sampled at landscape scales to determine the time-space variability in measured rates. Once this natural variability is determined, the models in this study can be

given a stronger context. The complexity of the year-to-year variation in evolution rates and the variability in the tropics suggest that no simple conclusions regarding the net effects of global warming will be forthcoming soon.

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GEOGRAPHICAL PECULIARITIES OF THE PRODUCTION — DESTRUCTION — PROCESSES IN NORTHERN EURASIA

NATALIA I. BAZILEVICH, ALEKSANDER V. DROZDOV, ROMAN I. ZLOTIN

Abstract. The new maps based on descriptions of 126 plant formations are introduced showing the patterns of phytomass, mortmass, net primary production and the ratio of mortmass to production in territory of Northern Eurasia. Geography of decomposition is explained in tables and the role of biotic and abiotic factors in this process rate is discussed. Two of analysed indexes, mortmass reserves and mortmass-productivity ratio response strong to meridional (west-east) climatic gradient in Northern Eurasia.

Key words: distribution of organic matter, latitudinal-meridional gradients, decomposition, primary production

The issue of productivity of the major landscapes of Eurasia and of the part of this largest continent that is within the former USSR was discussed in its general aspects in several monographs as early as in the 1960-es (Rodin, Bazilevich 1965), and introduced in form of small-scale maps (Bazilevich, Rodin 1971). However, in the recent two decades many new publications were issued; some of them were summarized in a volume specially devoted to this issue (Bazilevich, Grebenshikov, Tyshkov 1986), some — in the form of 4 maps compiled by N.I. Bazilevich in scale 1:8 000 000.

These new, not published maps include 126 plant formations found on the USSR territory, demonstrate the amount of phytomass and mortmass, net primary production and the ratio of mortmass-production. These maps were based on the vegetation map compiled by V.B. Sochava (1964) and modified by N.I. Bazilevich. All parameters were arranged in a 1-10 scale (Table 1) for better perception and comparison of the patterns.

Thanks to the more detailed scales and legends, the new maps show the zonal ecosystems widely spread over lowlands of Northern Eurasia (tundras, various forests, steppes, deserts), as well as the intrazonal formations, such as swamps, meadows, and also the major mountain ecosystems. For the first time total amount of dead phytomass (mortmass), i.e. the amount of vegetation debris in the aboveground and ground strata of ecosystems is mapped. A map showing the ratio of mortmass to net primary production gives a new understanding of the main features of the destruction phase in the biological cycle. More comprehensive information is provided on ecosystems of the polar zone, new data obtained with modern techniques are introduced on productivity of grasslands.

Table 1. Ten-level scale of productivity indices used in maps construction

Indices of productivity / Levels (points)	Phytomass $t \cdot ha^{-1}$	Mortmass $t \cdot ha^{-1}$	Annual production ANP $t \cdot ha^{-1} \cdot y^{-1}$	Ratio of mortmass to annual production
I	2.5	2.5	1.0	1.0
II	2.5-5.0	2.5-5.0	1.0-2.5	0.1-0.2
III	5.1-12.5	5.1-12.5	2.6-4.0	0.3-0.7
IV	12.6-25	12.6-25	4.1-6.0	0.8-1.5
V	26-50	26-50	6.1-8.0	1.6-5.0
VI	51-150	51-150	8.1-11.0	6.0-10.0
VII	151-300	151-300	11.1-16.0	11-15
VIII	301-400	301-400	16.1-30.0	16-20
IX	401-500	401-500	30.1-50.0	21-50
X	500	500	50.0	50

To give a generalized description of productivity of 126 plant formations, published and original data were collected for nearly 2000 sites. Comprehensive analysis of this huge mass of data is a task for nature. In this paper, we will limit ourselves to a general review of the above mentioned maps and comparison with the cartographic representation of the major factors of landscape differentiation in Northern Eurasia. Besides, we shall practically leave out mountain areas and shall only generally mention intrazonal ecosystems.

Geographical analysis of productivity of vast territories using small-scale maps is typically performed within the boundaries of large belts and zonal vegetation subdivisions. We will use here a grid of landscape zones and sectors (Fig.1) compiled on the basis of papers by F.N. Milkov (1977), A.G. Isachenko (1988), N.N. Rozov and M.N. Stroganova (1979) workers and subsequently combined with the vegetation map of V.B. Sochava (1964).

First, let us schematically describe salient features in the distribution of productivity indices, as presented in the four above-mentioned maps.

Highest phytomass reserves (Fig.2) are concentrated in broadleaved — coniferous and south-taiga forests in the west of the Russian Plain. All other forests[1] have higher-than-normal values, while typical and southern tundras, meadow-and true-steppes and northern deserts have medium-size reserves. Low values are typical for dry steppes, semi-deserts, true and southern (subtropical) deserts, while Arctic deserts have lowest phytomass reserves.

Highest reserves of mortmass (Fig.3) are accumulated in peat bogs which are mostly concentrated in Western Siberia, as well as in dwarf cedar and alder forests in Chukotka, Kamchatka and other mountaneous eastern regions. Higher-than-normal reserves are observed in all forests in the Pacific sector, northern taiga on the Kolyma, southern taiga in Central Siberia, as well as in the forest band on the Russian Plain and in Western Siberia, from central taiga to broad-

[1] With the exception of subtropical and all mountain forests which are not discussed in this or any other section of the article.

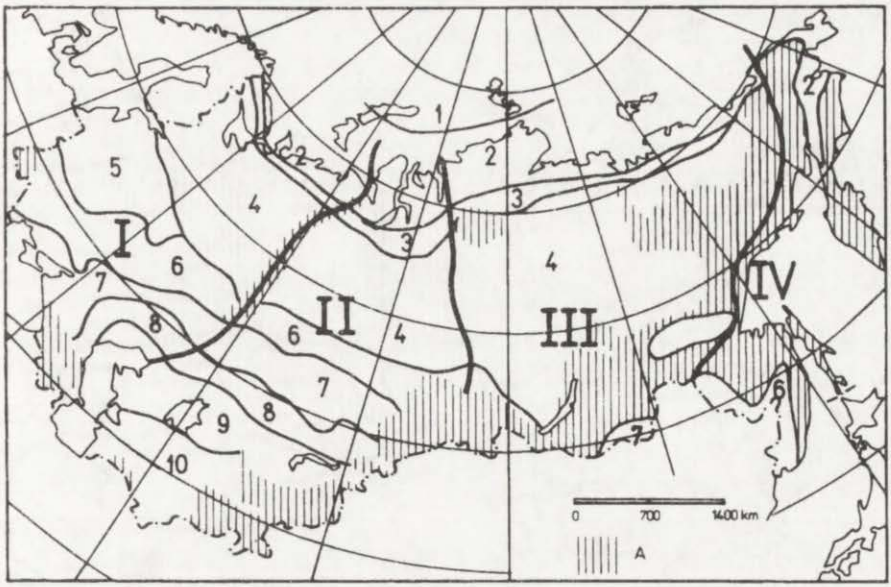

Fig.1. Pattern of landscapes differentiation in the Northern Eurasia (in the boundries of the former Soviet Union)

Landscape sectors: I. East-European, II. West-Siberian, III. Central- and East-Siberian, IV. Pacific. Main landscape zones: 1 – Arctic deserts; 2 – Tundra including arctic, typical and southern tundra; 3 – Forest tundra; 4 – Taiga forests (coniferous forests), including northern, middle and southern taiga; 5 – Broadleaved and coniferous forests (subtaiga); 6 – Forest steppe, including broad-and needle-leaved forests and meadow steppe; 7 – Steppe, including true and dry steppe; 8 – Semideserts; 9 – Northern (subboreal) deserts; 10 – Southern (subtropical) deserts.

leaved forests. Medium-size mortmass reserves are typical of all other forests, as well as meadow and true steppes, low values characterize Arctic deserts, dry steppes, semi-deserts and northern deserts, while the lowest values pertain to true and southern (subtropical) deserts.

Annual production (Fig.4) reaches highest values in meadow steppes of the forest-steppe zone and in true steppes. Higher-than-normal values are typical for southern taiga, broad-leaved-coniferous and broad-leaved forests, as well as for dry steppes; medium-size values characterize northern and central taiga on the Russian Plain, central and southern taiga in Siberia and semi-deserts. Low values are typically observed in tundras, all other forests, true and southern (subtropical) deserts, while Polar deserts and northern deserts have the lowest values.

It is the ratio between mortmass and annual production (Fig.5) that exhibits the smallest spacial variation. The ratio is the highest in Vasyuganye peat bogs in Western Siberia, higher-than-normal in Siberian forest-tundra and northern taiga, moderate values are observed in typical and southern tundras, forest-tundra and northern taiga on the Russian Plain, in middle taiga, as well as in southern taiga of Central Siberia and Pacific sector. The ratio has low values in Arctic deserts and typical tundras of Siberia, in southern taiga in the European sector, in all

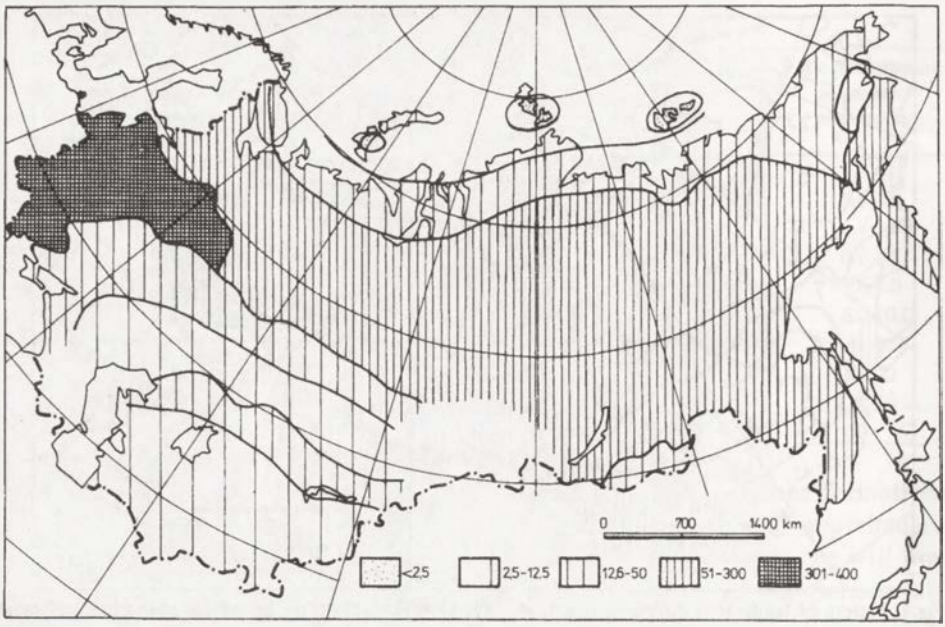

Fig.2. Geographical differentiation of phytomass reserves in Northern Eurasia ($t \cdot ha^{-1}$)

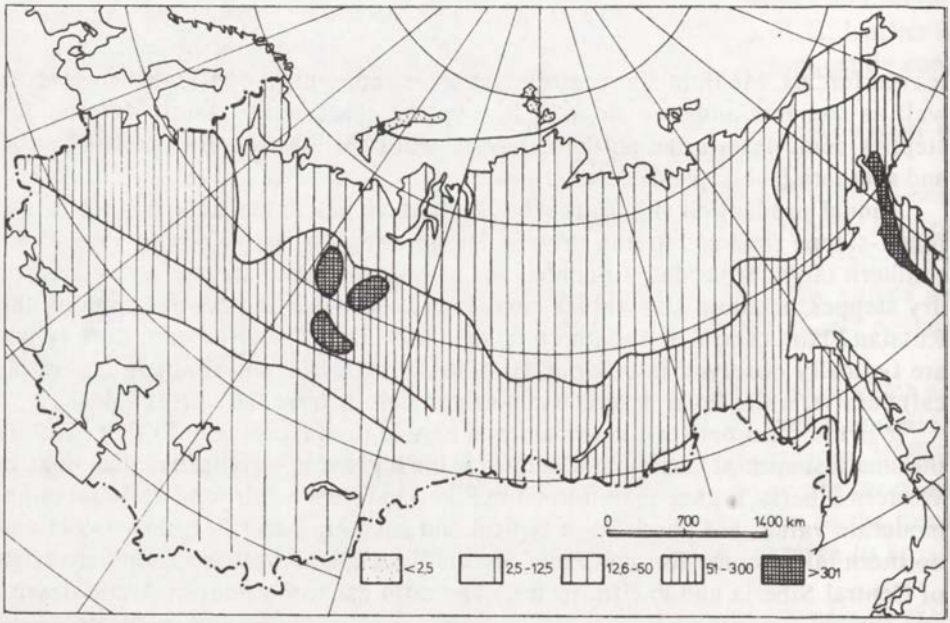

Fig.3. Geographical differentiation of mortmass reserves in Northern Eurasia ($t \cdot ha^{-1}$)

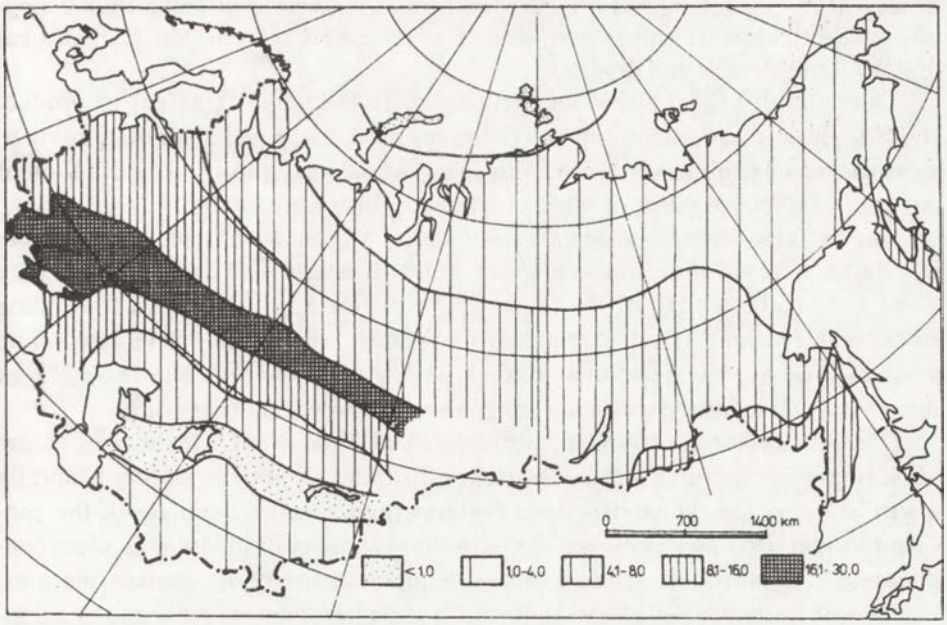

Fig.4. Geographical differentiation of ANP (annual net production of plants) in Northern Eurasia ($t \cdot ha^{-1}$)

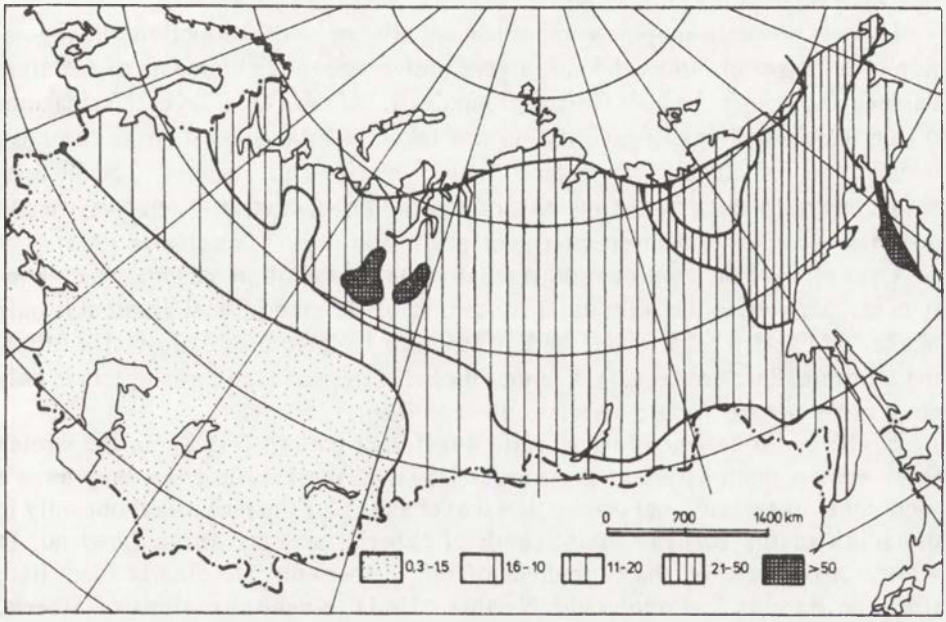

Fig.5. Pattern of geographical distribution of the ratio mortmass: ANP in Northern Eurasia

broadleaved-coniferous and broadleaved forests, as well as in Trans-Baikal steppes, while the lowest values pertain to vast steppes (except in the Trans-Baikal region), semi-deserts and deserts.

Thus, besides the wellknown north-south or latitudinal gradient of productivity indices, these rather generalized maps are clearly demonstrating another, west-east, or meridional gradient. This is most obviously shown in distribution of mortmass and of the ratios of mortmass to net primary production.

One can also trace a belt or axis common for all four maps that stretches from the Baltic Sea via the Southern Urals to the Western Altai, or approximatley along the southern edge of the taiga. South of this edge, there is a most clear latitudinal gradient of all parameters of productivity under discussion, while north of this axis the meridional gradient is more pronounced. Besides, south of this axis on all maps the gradients are generally sharper that north of it.

Does this rather generalized pattern agree with the general features of nature of Northern Eurasia and with its landscape differentiation? The answer generally is yes, it does. The above described features registered on the maps of the continent reflect, first and foremost, the latitudinal zonality of landscapes, clear continentality of Northern Eurasia, and oceanic regimes of its eastern margins. Division of landscapes into humid and arid is also clear; they are separated by a transitional zone of forest steppes coinciding with the above mentioned gradient axes.

Therefore, a more detailed geographical analysis of productivity parameters should be carried out for the network of landscape zones within individual meridional sectors, and also for groups of humid and arid landscapes. Let us start this analysis with the most important climatic group of factors.

Usually, the cartographic comparisons of climate with productivity of vegetation at the level of landscape zones give preference to the elements of radiation balance and to one of many indices of humidity. At the global level the measures of air temperature and precipitation are taken into consideration as the most widely observed climatic parameters. These parameters are assumed to be the driving factors of productivity of phytocenoses in the global models. Therefore, we will undertake a review of the respective general climatic maps (Mjatschkova 1983).

Over most of the continent the annual values of radiation balance are regularly corresponding to the latitudinal zones (Fig.6). The meridional gradient is only marked in Eastern Siberia and the Far East. Air temperatures of July also follow the latitudinal pattern (Fig.7). The meridional pattern of the July isotherm is only observed along the Pacific margin of the continent.

Isotherms of January follow quite a different pattern (Fig.8): in the stretch from western boundaries of the former USSR to the Pacific coast they have a predominantly meridional orientation that changes for the latitudinal one only in the south of the Russian Plain, south of Siberia, and the Turan Lowland. In winter three areas of sharp gradient of the temperature are clearly identified: from the Barents Sea across the Northern Urals to central regions of Siberia, north of the Caspian, and along the Pacific coast. Thus, the influence of warm

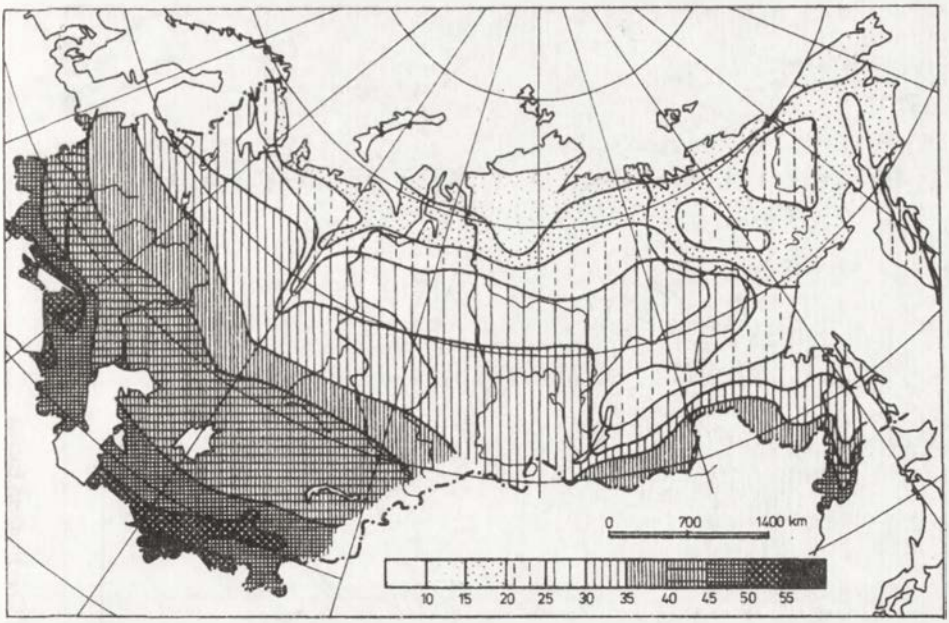

Fig.6. Annual values of solar radiation balance in Northern Eurasia ($Kcal \cdot cm^{-2} \cdot y^{-1}$)

sea water masses is very clear in the winter thermal patterns over Northern Eurasia.

The precipitation over the territory (Fig.9) shows both the latitudinal and meridional gradients. The absolute minimum of precipitation (less than 200 mm per year) is associated with the zone of southern deserts. The other relative minimum (200-400 mm per year) occurs over the vast space of Central and East Siberian taiga and tundra. The eastern margin of the continent, the Western Siberia and the Russian Plain get 600-1000, 400-600 and 600-800 mm per year of precipitation, respectivelly. Thus, the field of precipitation over the territory north of 50 NL, with exclusion of a narrow tundra stripe, shows clear meridional sectors (see Figs 1 and 9).

Despite significant contrasts in the 4 sectors north of the forest steppe zone, the values of evapotranspiration are close (Fig.10). Forest steppes coincide with maximum of evaporation, while semideserts located further south have the highest gradients of the evaporation field.

The zone of forest steppe is also coinciding with the line of zero difference between precipitation and potential evaporation (Fig. 11). South of it is the area of moisture deficiency (up to 1500 mm per year in southern deserts), northward is the area of excessive moistening. The only exception is the vast taiga-grown South-Yakut depression with the summer moisture deficiency of about 100 mm per year. In combination with extremely low winter temperatures, this accounts for high continentality of climate in this area.

These are the general features of spatial climatic patterns in Northern Eurasia

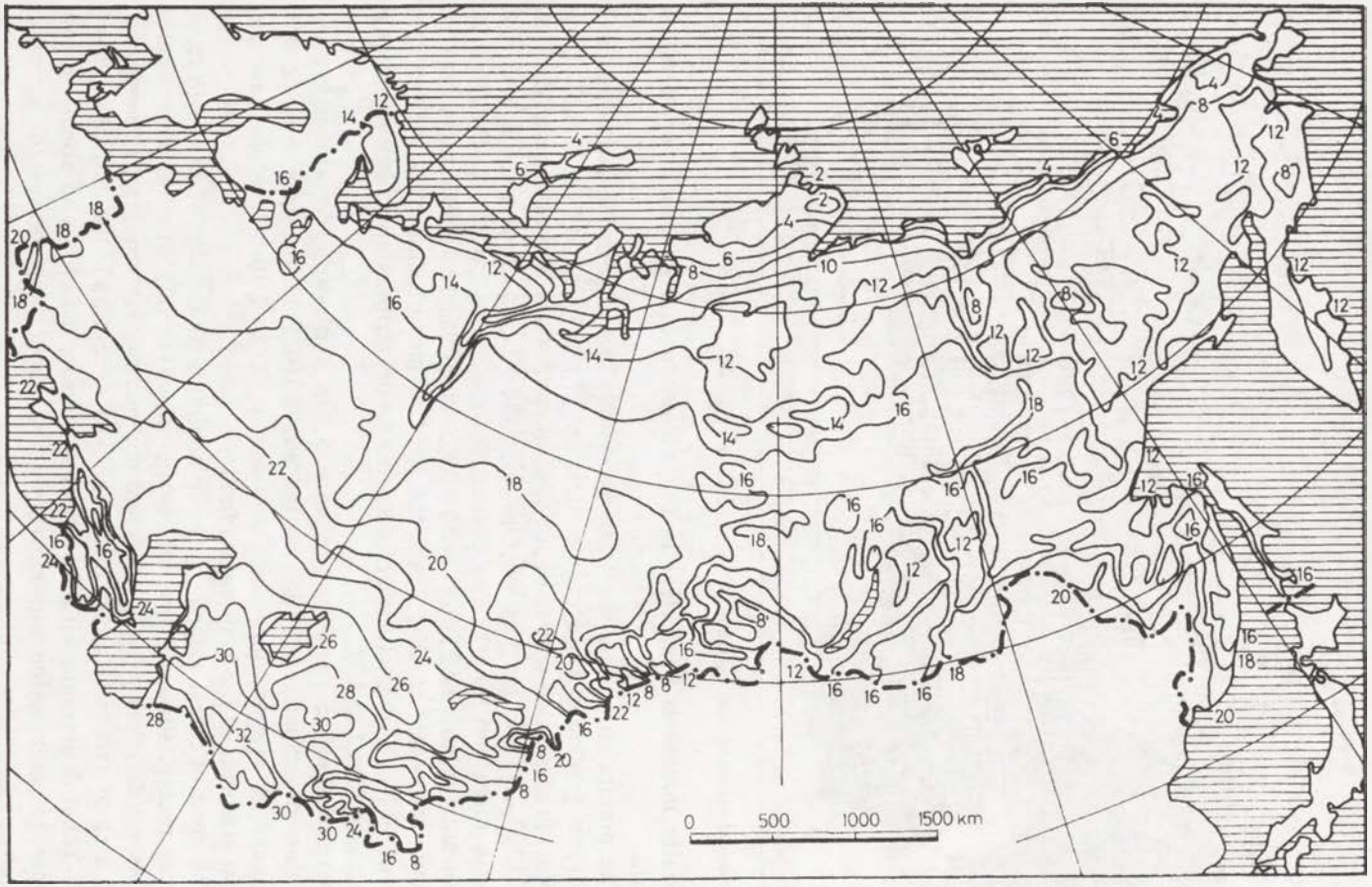

Fig.7. Mean air temperature of July (°C) in Northern Eurasia

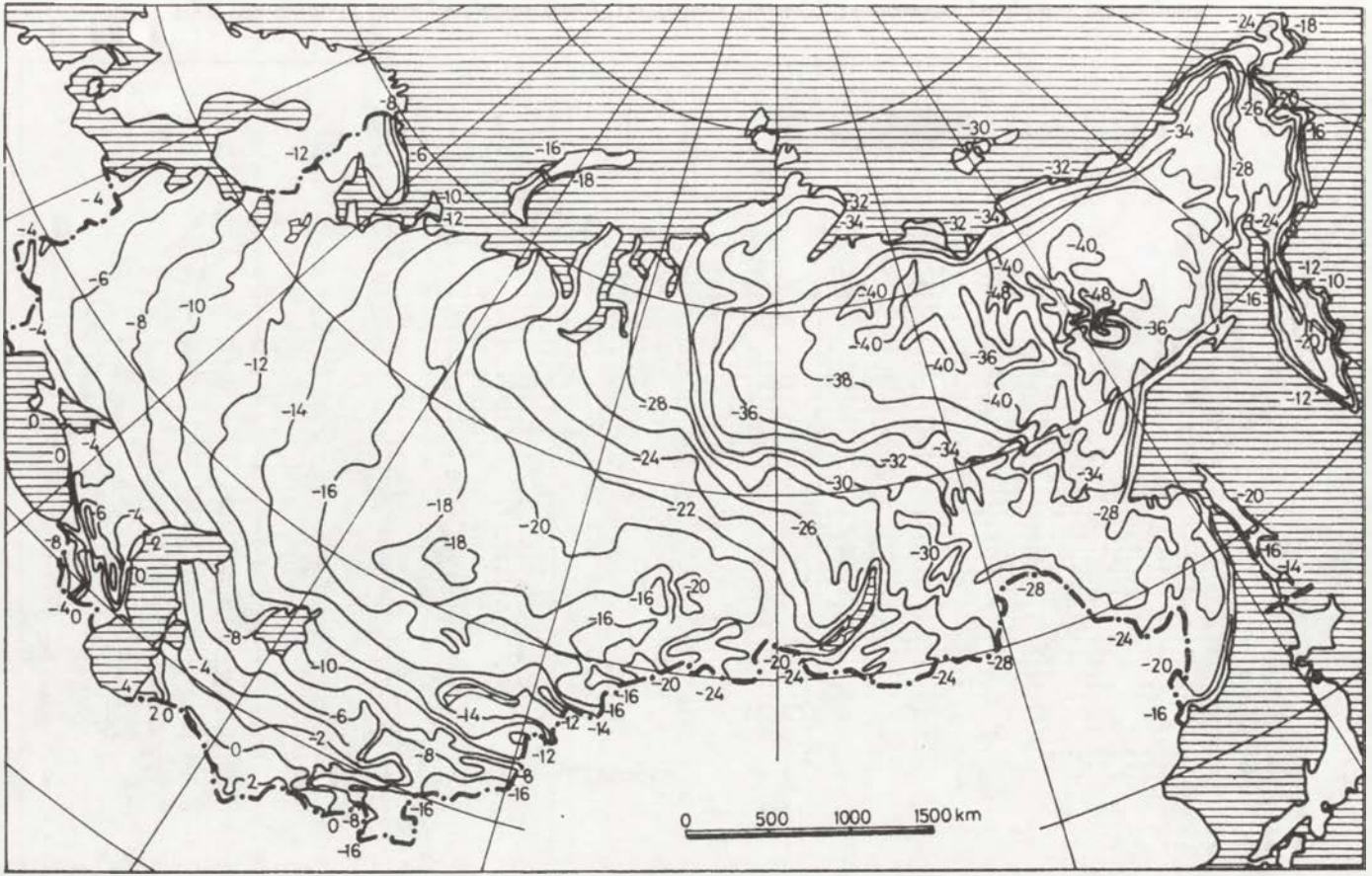

Fig.8. Mean air temperature of January (°C) in Northern Eurasia

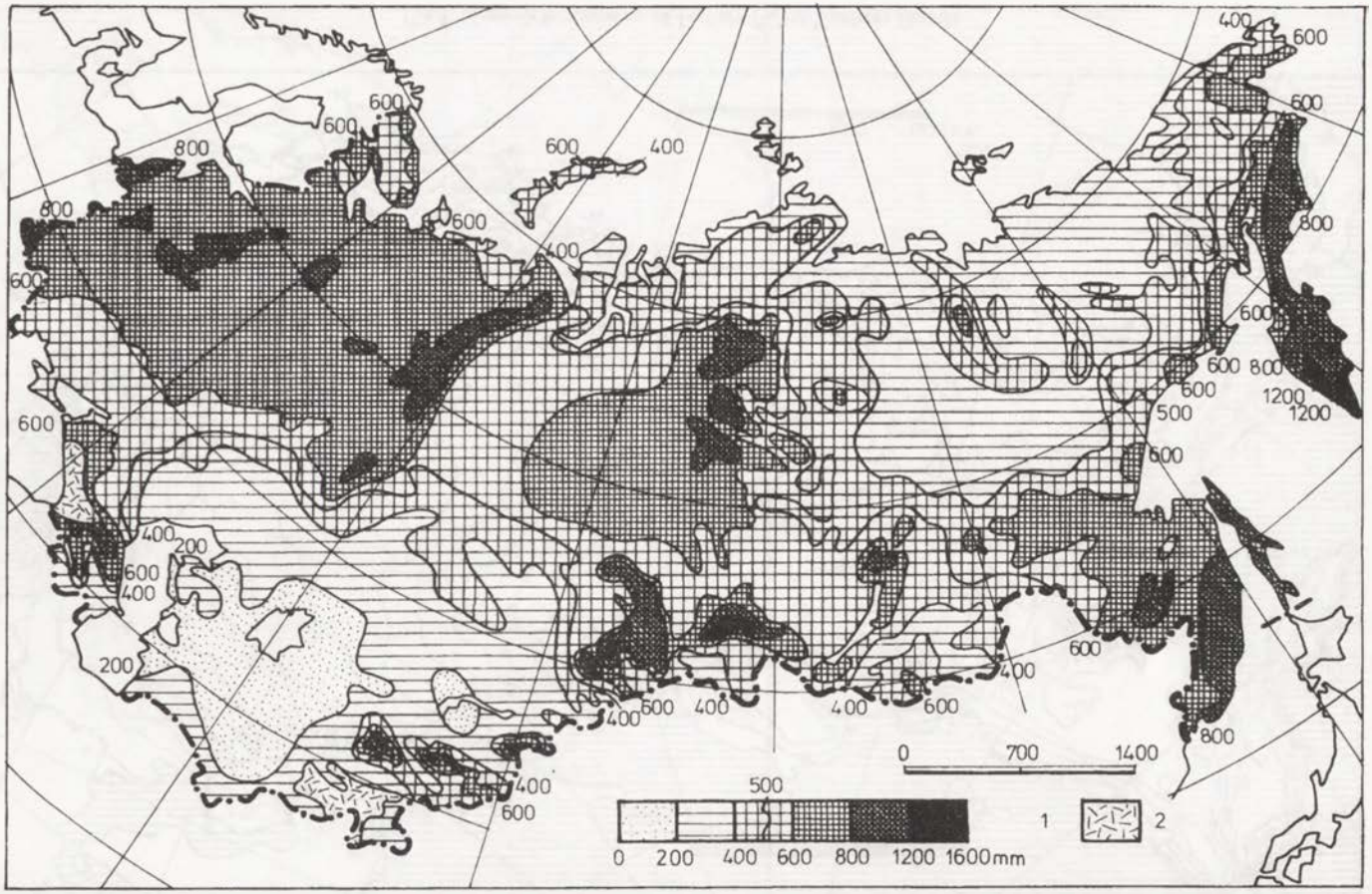

Fig.9. Distribution of annual precipitation (mm·y^{-1}) in Northern Eurasia(1); 2 – mountains, precipitation not computed

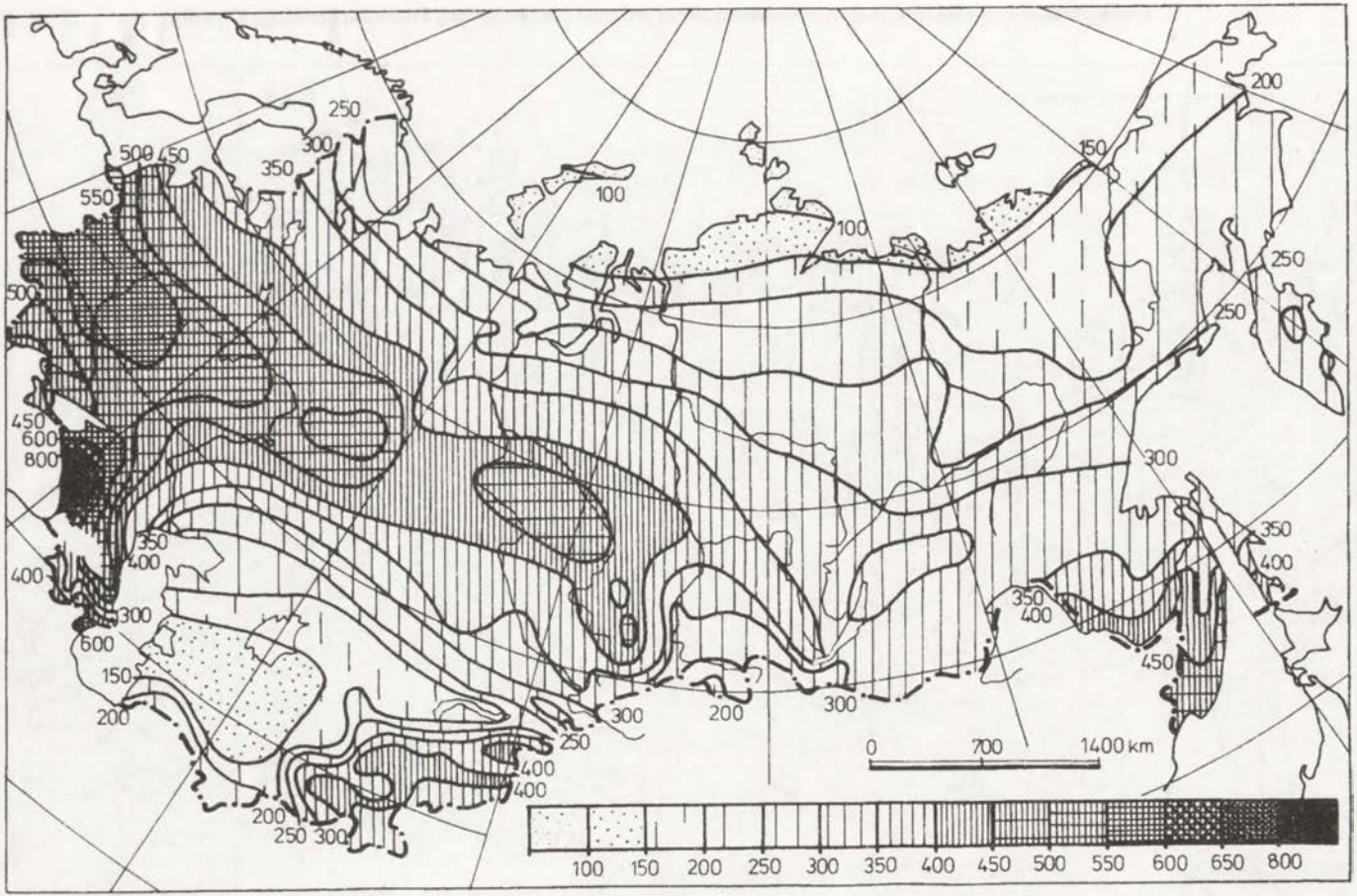

Fig.10. Evapotranspiration distribution in Northem Eurasia (mm·y^{-1})

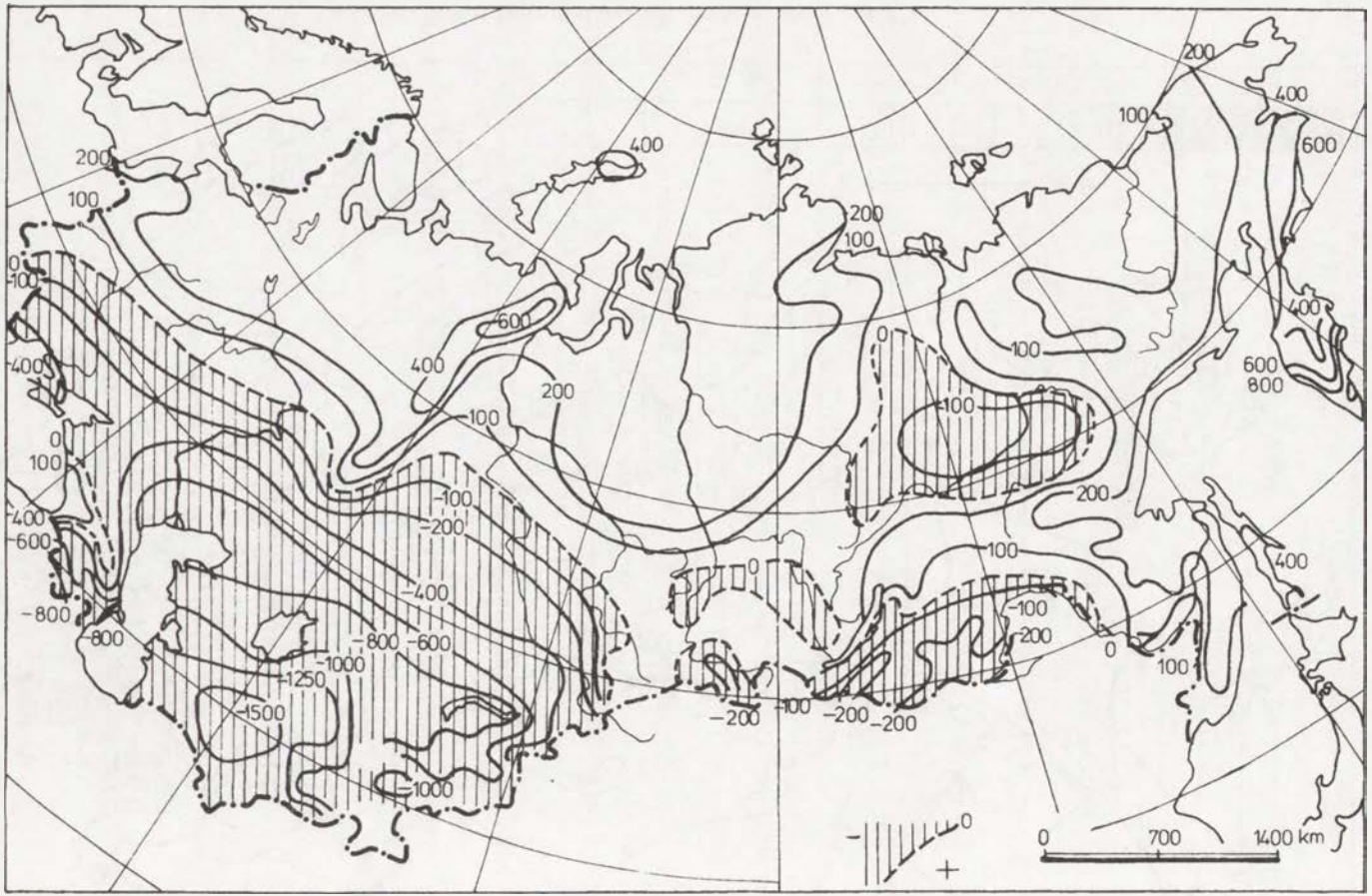

Fig.11. Differences between precipitation and potential evapotranspiration (mm·y^{-1}), pattern in Northern Eurasia

within the former USSR. These peculiarities essentially account for the spatial patterns of the vegetation cover and productivity in the area. There are some quite successful attempts to employ these explanations for constructing the map-models of productivity (Yefimowa, 1977; Zubov 1978). The map-model of S.M. Zubov (1978) constructed on the basis of correlations of plant communities production, radiation balance and precipitation, showed no strong sectoral pattern of productivity or special patterns in arid landscapes. Obviously, besides these climatic factors, other characteristics should be taken into account, including the specific climatic parameters determining the spatial patterns of productivity. One of such parameters relevant for the extremely continental cold Northern Eurasia is soil temperature (Fig. 12).

In relation to the other two western meridional sectors, the taiga forests of Central and Eastern Siberia are characterized by lower annual production of living phytomass (Fig. 13). The reasons for this are, on the one hand, extremely low winter temperatures and the negative mean annual temperatures of the soil, and, on the other hand, arid climate of the summer months.

In general, the sectoral changes of all the parameters of productivity within the major landscape zones, shown on Figs 13 and 14 may be explained by climatic characteristics of the sectors. The peculiarity of the Pacific sector should be noted first of all. Here the oceanic influence on the cold and moderately cold climate substantially reduces the zonal contrasts. A contrary picture is characteristic of the European sector, where in accordance with the high climatic changeability, the greatest inter-zonal contrasts of the productivity parameters are being observed.

The intersectoral changes of these parameters within the boundaries of separate zones are also peculiar. In this context two landscape zones particularly stand out — the forest tundra and the forest steppe (the latter is characterized by the productivity of the meadow steppes, situated within its boundaries, on Figure 13 and 14). They both are notable for very low inter-zonal changes of the living phytomass and mortmass volumes, of the annual production and the relation of the mortmass to the production. In the forest zone, situated between the forest tundra and forest steppe ecotones, some general tendencies of change become apparent from west to east: a decrease of living phytomass volume and annual production with the increase of the relation of mortmass to production. A different general tendency reveales itself in the typical dry steppes and in the tundra; in the Central Siberian sector these zones are characterized by elevated volumes of the living phytomass. It would be interesting to reveal the reaction of other ecotone ecosystems to climatic changes — probably, all the ecotones are characterized by a certain permanency of the productivity parameters.

It is necessary to note, that the semidesert and desert zones are not represented on Fig. 13 and 14, because within their boundaries the intersectoral changes of the productivity parameters are far from obvious. The reason is that these extremely arid zones are almost equally continental along their whole length. The role of the spatial diversity of climate here seems to be less important, than the role of other factors. So, the subboreal Kazakhstan semideserts by all the produc-

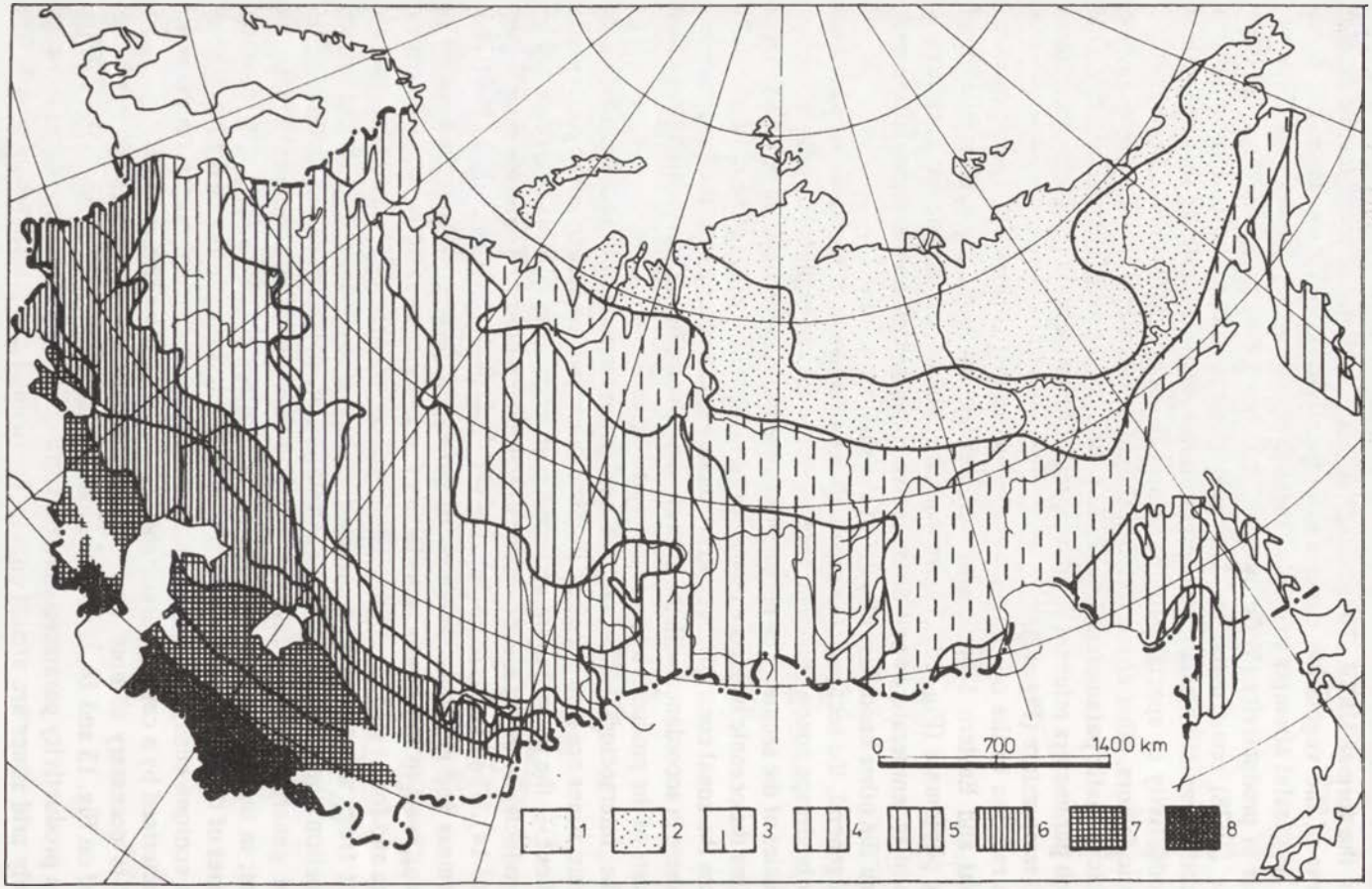

Fig.12. Mean annual soil temperatures (°C) measured at the depth 20 cm (After V.N. Dymo 1967)
1: 16 – 20°C; 2: 12 – 16°C; 3: 8 – 12°C; 4: 4 – 8°C; 5: 0 – 4°C; 6: -4 – 0°C; 7: -8 – -4°C; 8: -12 – -8°C

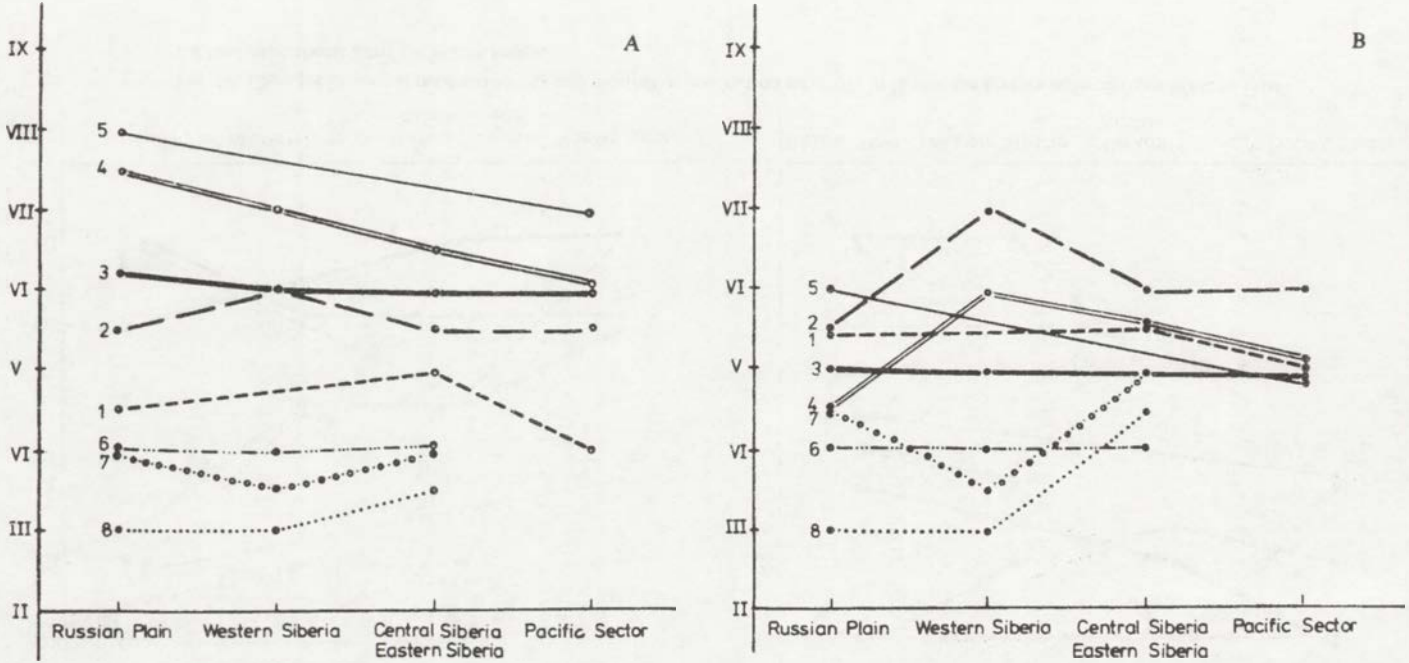

Fig.13. Changes in productivity indices in landscape sectors from West to East

1-8 landscape zones; A– phytomass; B– mortmass; Zone No 7– true steppe. Values of indices acc. to Tab. 1.

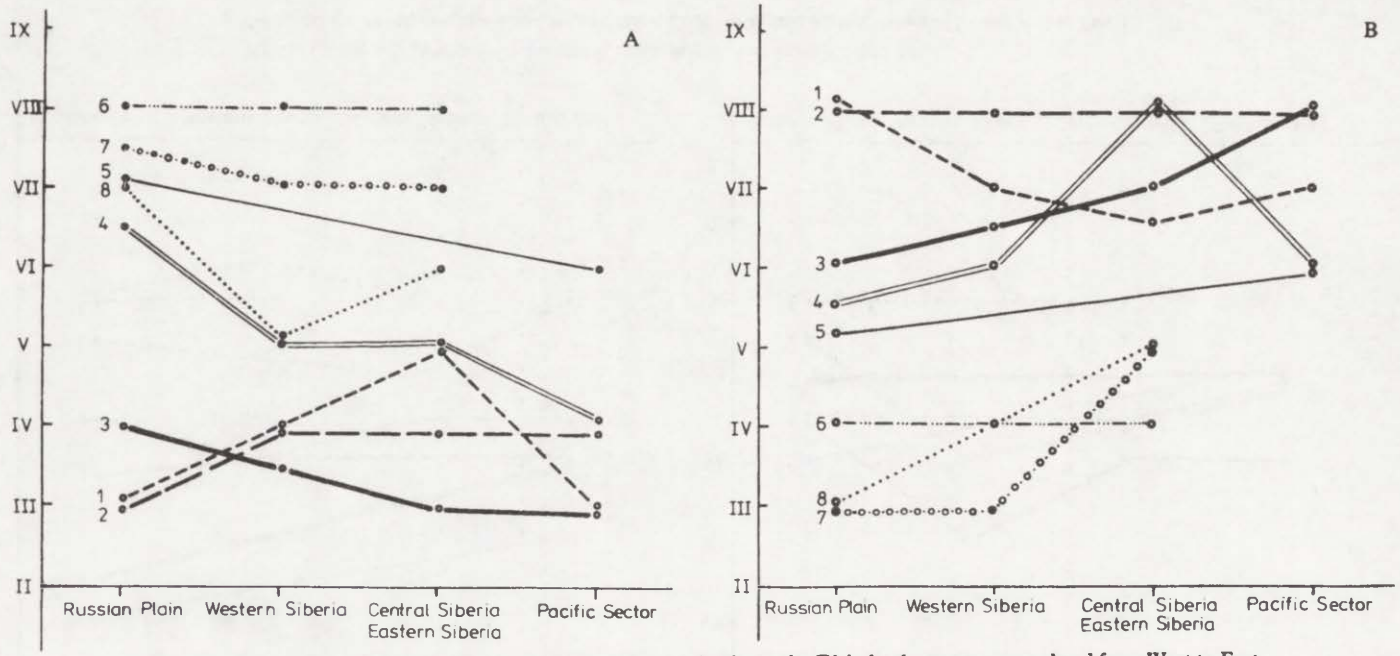

Fig. 14. Changes in annual production (A) and mortmass: production ratio (B) in landscape sectors ordered from West to East
1-8 landscape zones; Zone No 7- true steppe.

tivity parameters in question are practically identical to the subtropical semi-deserts of Azerbaijan, even though they are situated in different climatic zones[2]. But the subboreal arid deserts with clay and sand soils differ drastically (Table 2).

Table 2. Productivity of hot deserts on clayey and sandy soils

Vegetation formations	Productivity indices evaluated by numbers			
	alive phytomass volume	mortmass volume	annual primary production	ratio "mortmass: production"
Artemisia kemrudica *Anabasis salsa*, clay	II	I	I	IV
Haloxylon persicum *Calligonum*, *Ephedra*, sand	III	II	II	III

Along with the substratum, the other important factors regulating arid landscape productivity are the underground water, the mineralization of the water and also the salinization of the soil and ground. In general, the role of the bedrock and the soils conditioning the mineral supply of the vegetation is very important in many regions. Volcanic regions or oceanic coasts with their special geochemical conditions may serve as examples (Bazilevich 1981).

The climate should be considered a leading factor of vegetation productivity only on certain scale investigation (first of all, global and continental), and by far not in all types of environment.

The data analysed earlier by M.V. Udalkina, N.I. Bazilevich and others (1988), make it possible to illustrate the relative role of climate in the change of productivity of various plant communities in the taiga zone (Table 3). As shown in the table, within the taiga landscape zone the change of air temperature influences forest productivity more, than the change of percipitation. At the same time the sensitivity of different communities is not equal. The pine has the lowest, the larch — the greatest; the sensitivity to temperature change is higher in the poly-dominant forests, while spruce forests react relatively faintly only to the change in percipitations.

In this context it is interesting to observe the change of productivity with the zonality gradient in pine — cowberry communities (*Pinus silvestris* — *Vaccinium myrtillus*). Compiled with the use of materials from the monograph of V.N. Gabeev (1990), table 4 contains the data on the main parameters of productivity of pine forests of Western Siberia, situated in the zones of taiga, forest steppe and steppe. In all the cases these pine forests grow in well drained habitats and only in the steppe zone they probably get additional ground moisture. It is rather easy to notice that the zonal distribition of the productivity indices: the annual production and annual needle fall of these pine forests, corresponds in general to the laws of all the other forest communities.

[2] It is necessary to recognize a certain vagueness of the borders between climatic zones. That is why in this article, in accordance with the scale of the undertaken cartographic analysis, we deal mainly with the zonal division of landscapes.

Table 3. Annual production changes (%) of the taiga forests with the change of air temperature and precipitation

Taiga forest types	Production change	
	with 1°C of mean annual air temperature change	with 1% of annual total precipitation change
Spruce (*Picea*)	no considerable change	2.55
Pine (*Pinus*)	no considerable change	0.45
Larch (*Larix*)	9.4	no considerable change
Coniferous polydominant (*Picea* + *Abies* + *Pinus*)	10.1	0.67

Table 4. Productivity of the pine forests of Western Siberia (after Gabeev 1990)

Zone and subzone	Productivity indices in ton per ha				Ratio "mortmass: production"
	Alive phytomass	Mortmass	Annual production	Annual needle fall	
Taiga					
north	849.3	243.4	28.8	21.9	8.4
middle	2083.4	270.9	49.9	37.2	5.4
south	2960.4	404.9	56.4	40.8	7.2
Forest steppe	2001.7	437.7	46.4	35.8	9.4
Steppe	1313.8	626.4	37.0	23.1	16.9

A relatively wide range of inter-zonal changeability of parameters sometimes reaching 200 to 300% also attracts attention. It is true, however, that the annual climatic characteristics change greatly in this zonal row also — the radiation balance varies from 30 to 40 kcal · cm^{-2}, the precipitation from 600 to 350 mm, the difference between precipitation and potential evaporation from +200 to -200 mm.

Apparently this does not contradict the conclusion about the relatively poor sensitivity of the pine to climatic changes; it only demonstrates the complexity of the connections between the productivity and the regulating factors and also the necessity to study them closely.

The geographical approach to such an investigation should consist first of all, in the re-evaluation of universal connections between the productivity of ecosystems and the main, directly acting factors of physical, chemical and biological nature — all these on different analysis scale and in different types of environment. On the other hand, it is necessary to reveal indirect factors, which determine the conditions and the character of the universal connections.

One of the means of revealing general relations of the "productivity — climate" phenomena could probably be the analysis of the zonal catena diversity on the slopes of northern and southern exposition.

The general mechanism of the influence of the heat and moisture on the phytocenosis productivity, corresponding to the principle of the limiting factor of Libich, reveals itself not only on the global — regional scale of the landscape zones, but also on the local scale of catenas. A different mechanism of the influence of these factors is characteristic of the forest steppe zone — here on the

slopes of different exposition the heat and moisture become not limiting, but compensating factors (Drozdov 1983).

Another aspect of the catena productivity analysis is the comparison of the interzonal changeability of watershed and bog habitats, the latter being the last element of a catena. As we could see from Fig. 15 (Bazilevich at al. 1986), bog production increases with the growth of radiation balance in the cold-humid and warm-arid landscape zones.

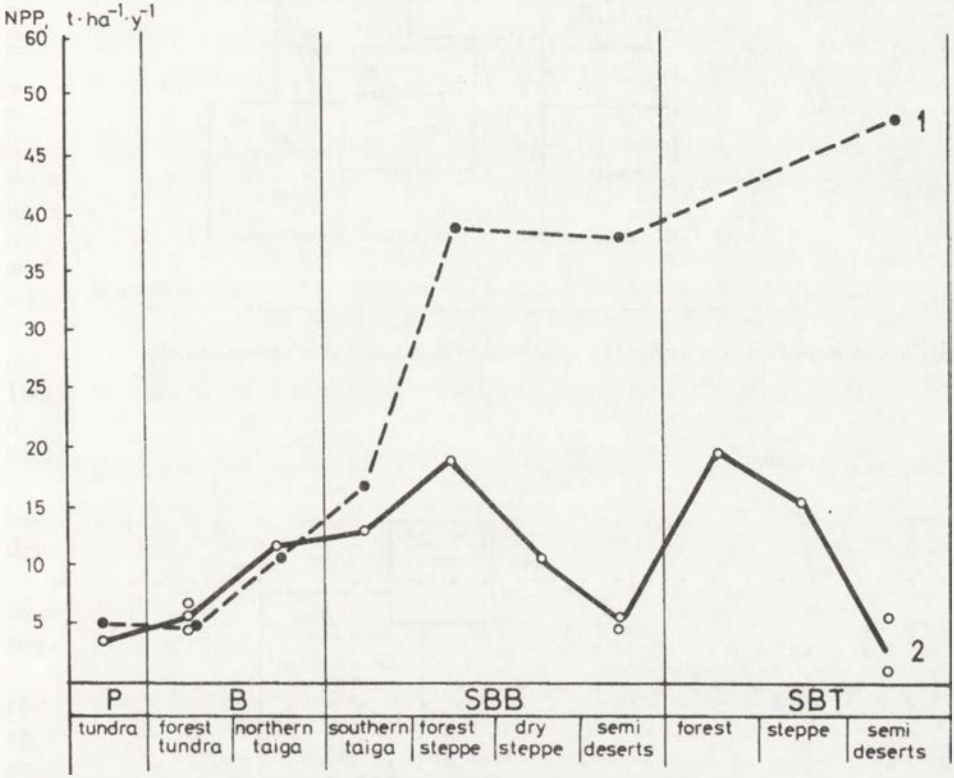

Fig.15. Zonal and azonal geographical pattern of the annual production in landscape zones
P — polar; B — boreal; SBB — subboreal; SBT — subtropical 1— bogs; 2 — watersheds

In accordance with the widespread interpretation of the productivity concept, and as it follows from the context this article, mortmass volume is one of the productivity parameters. Describing the relation between productivity, mortmass volume and environmental factors we in general describe the production and destruction processes. All the more, previously discussed spatial distribution of the ratio mortmass volume to annual production, is in fact the character reflecting the speed of the destruction processes.

In the distribution of this character, the west to east gradient is the most ap-

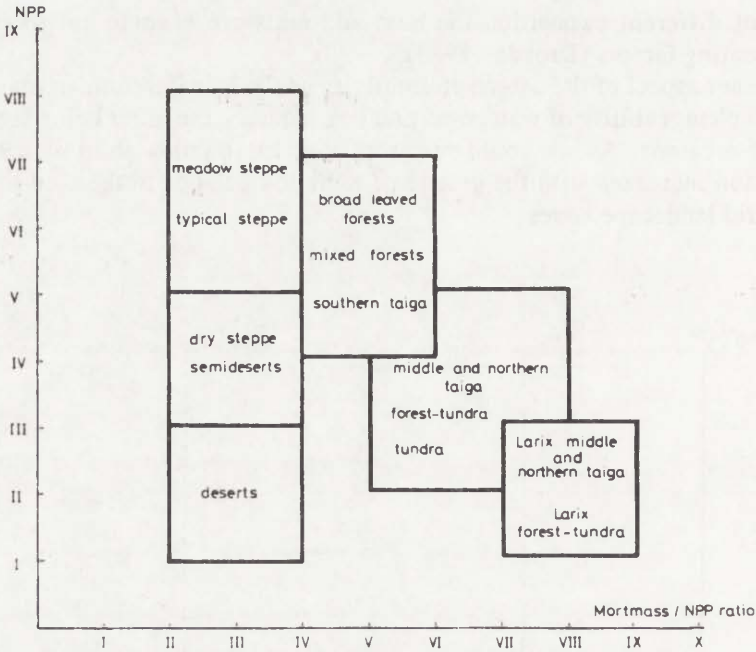

Fig.16. Landscape clusters in relation to productivity (NPP) and mortmass: production ratio

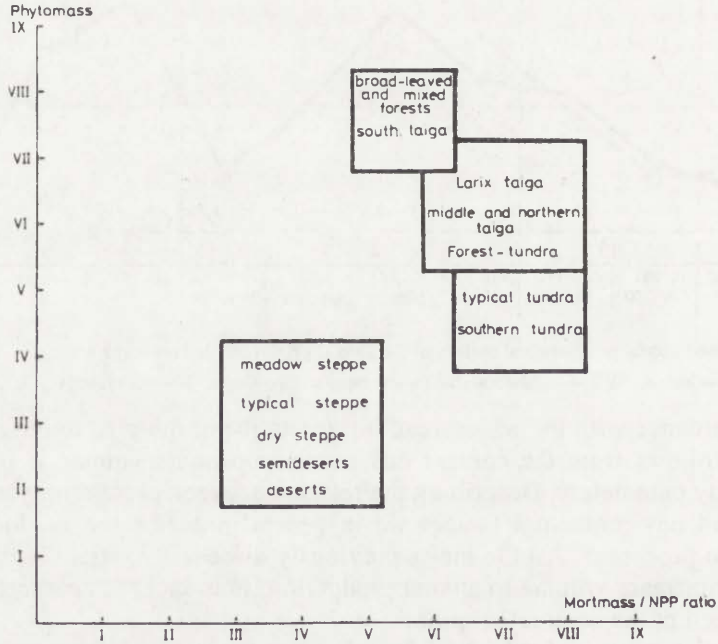

Fig.17. Landscape clusters in relation to phytomass reserve and mortmass: production ratio

parent (Fig. 5), even though it does not seem to be directly linked with the climatic factors. However, more detailed data presented in Fig. 16 and 17 suggest of noticeable differences in the two columns of plant formations. One of those has similar values of the mortmass production ratio for different values of production. In Fig. 16 this vertical column consists of desert, semi-desert and steppe formations, including meadow steppes in the forest-steppe zone. In the other column (from broad-leaved forests to forest-tundra and tundra formations) the ratio grows with the decline in production values. Forest steppe occupies a place of its own, since it seems to belong to both columns.

The same can be seen in Figure 17 which is to demonstrate differences between forest, forest-tundra and tundra landscapes.

Both, Figure 16 and 17 clearly suggest that the analysis of links between productivity features and environmental factors should be performed separately for humid landscaped and semi-arid and arid landscapes. In humid forests formations the rate of destruction is highest in warmest broad-leaved communities and lowest in the coldest larch forests of Siberia, while in semi-arid and arid landscapes the rate of destruction remains constant in all zones from true steppes, with the annual radiation budget of about 40 Kcal $\cdot$ cm^{-2}, to subtropical deserts, where the annual radiation budget averages to 50 Kcal $\cdot$ cm^{-2}.

The role played by climatic factors is indirectly manifested in a link between the mortmass/production ratio and absolute values of annual production (Fig. 16): the higher the production in humid landscapes, the higher the rate of destruction processes, since both, the production and destruction limbs of the biological cycle are dependent on energy in ecosystem processes.

Is the hydrothermal axis which roughly follows the southern forest-steppe boundary an important landmark separating landscapes with totally different development of destruction processes?

We are going to supplement this general cartographic analysis of the intensity of destruction processes with a description of field experiments whose results show specific rates of organic matter decomposition in different landscapes.

We distinguish two groups of factors controlling destruction processes in terrestrial ecosystems: biotic and abiotic. Biotic factors include above all different saprotrophic organisms (invertebrate and vertebrate animals, microorganisms) mostly inhabiting soil and litter, as well soil-enzyme reactions. Interestingly, many typically phytophagic animals, such as ungulates and certain rodents can be regarded as saprophagous in the cold season, when, in absence of green fodder, they turn to standing dead plant material and litter. Microbial-zoological interactions frequently stimulate the intensity of organic matter destruction processes.

Abiotic factors include leaching, photochemical oxidation and mechanical reactions brought about by the freezing and melting of organic matter.

One can discover certain regular features in the ratio between, and the degree of manifestation of various abiotic and biotic factors (Zlotin 1979; Zlotin, Khodashova 1980). Traditionally, the destruction processes in the biological cycling are believed to be controlled by biota. Hovever, one should bear in mind that abiotic factors are most effective in above ground layers, while biotic factors are more effective in underground ones.

Photochemical oxidation caused by direct short-wave solar radiation is an important factor of abiotic destruction. Consequently, in conditions of long duration and high intensity of solar radiation, including the short-wave part of its spectrum, photochemical reactions prevail in destructive processes. This applies to arid and semi-arid landscapes (deserts, steppes), to continental uplands and Polar regions. In humid forests, leaching becomes predominant among abiotic factors. Mechanical destruction plays an important role in areas with an insignificant snow-cover and with highly variable weather resulting in alternate freezing and melting of soil. The share of water soluble compounds in mortmass is not high, therefore the amount of annual leaching does not exceed several per cent. Mechanical destruction might have but a slight direct impact, but it facilitates decomposition when in conjunction with other abiotic and biotic factors.

One of the most simple, universal and widely used field methods for assessing the rate of destructive processes consists in burying cotton stripes (cellulose) in soil and in subsequent assessment of the degree of its decomposition through loss of weight or strength. This method allows, above all, to determine the microbiological activity in the underground layer of ecosystems (Zlotin, Chukanova 1973). Usually this process plays a substantial and, in certain cases, a prevailing role in destructive processes. Therefore, relevant experimental data provide convincing evidence for geographical analysis.

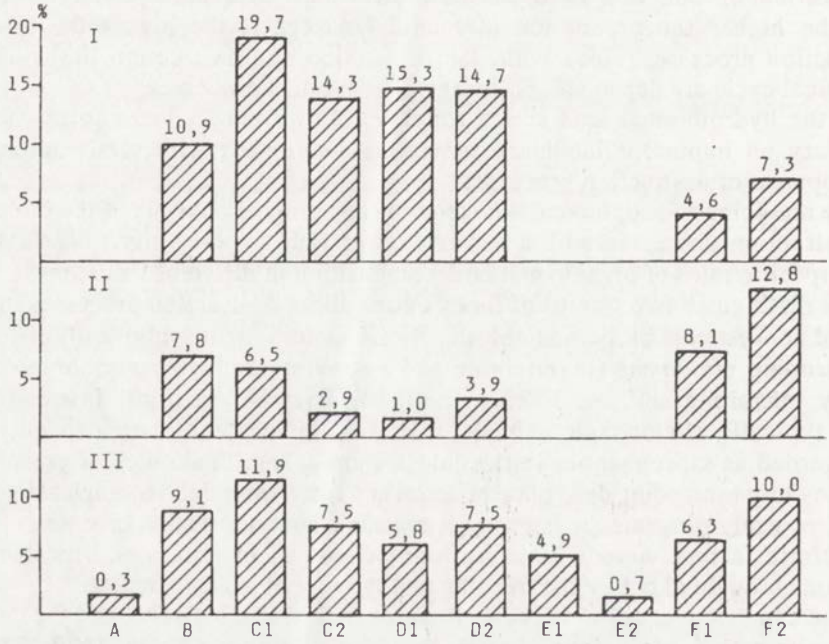

Fig.18. Geography of the rate of cellulose decomposition (% monthly, 0-30 cm soil depth)

I — warm season; II — cold season; III — year; A — arctic tundra; B — southern taiga; C — forest-steppe: C1 — oak forest; C2 — meadow steppe; D — true steppe: D1 — true steppe at the wastershed: D2 — oak forest in the ravins; E — desert: E1 — under Artemisia; E2 — open site; F — north savanna (pistachio open woodland): F1 — under pistachio; F2 — open site

Fig. 18 shows seasonal and annual variation in the decomposition of cellulose from the Polar to the Subtropical belt, presenting averaged results of field experiments conducted in each of the landscape zones in question for several years. In arctic tundra and in true deserts the experiment covered the entire year cycle, while in other zones the warm and the cold seasons were covered separately. In this last case annual values were calculated.

In contrast to zonal variations in the "mortmass/production ratio" whose values constantly decline from Polar ecosystems to subtropical ecosystems, cellulose decomposition in soil change in a slightly different manner along the north-south gradient.

In the warm season, highest destruction rates are observed in forest-steppe (primarily in oak forest) landscapes, while lower values are typical both for more humid (south taiga), and more arid (steppe and xerophytic light forests) landscapes. This might be attributed to the optimal moistening conditions in forest-steppe and lack of moisture in steppes and pistachio — light forests. As for south taiga, it must be lack of heat which comes into play.

In the cold season, the lowest values of destruction intensity are observed in true steppes, while meadow steppes and forest landscapes have higher values. One can suggest that such differences are caused by the low temperature of soil in winter, which freezes deep enough in open steppe landscapes and remains almost unfrozen in oak forests in forest-steppe and in south taiga.

On the whole, the values of destruction in winter are everywhere much lower than in summer. The only exception is xerophytic pistachio — light forests which are characterized by typically subtropical Mediterranean pattern of precipitations — dry summer and moist winter with rare and short cold spells against the above-zero background.

As for zonal series of annual destruction cycle, this exhibits two areas with minimal values. They are arctic tundras and north deserts. The lowest microbial activity and destruction of the both landscapes must be attributed to lack of heat in the first case and to lack of moisture — in the second case. The value of cellulose destruction is high in south taiga and in oak forests of forests-steppe, both in the annual and in the two seasonal cycles. In general, the distribution of annual destruction values along the north-south gradient is very much similar to those of annual primary production.

One should also note that the values of destruction under the cover of oak forests are typically higher than on open grasslands in forest-steppes and true steppes; the same is observed in the north deserts, where the rate of decomposition is much higher under Artemisia bushes than on open exposed sites. This must be due to higher degree of soil moistening under the cover of the forest because of snow accumulation.

A more detailed pattern of seasonal variations in cellulose decomposition rate in different soil layers and on the litter in East European forest steppe landscapes (Fig. 19) also highlights the primary role played by hydrothermal factors in this mainly microbiological process. The rates of destruction in the warm and cold

seasons differ by a factor of 4-5 in oak forests and by a factor of 5-6 (Fig. 19) in meadow steppes, which corresponds to seasonal contrasts of temperature in those forest-steppe ecosystems.

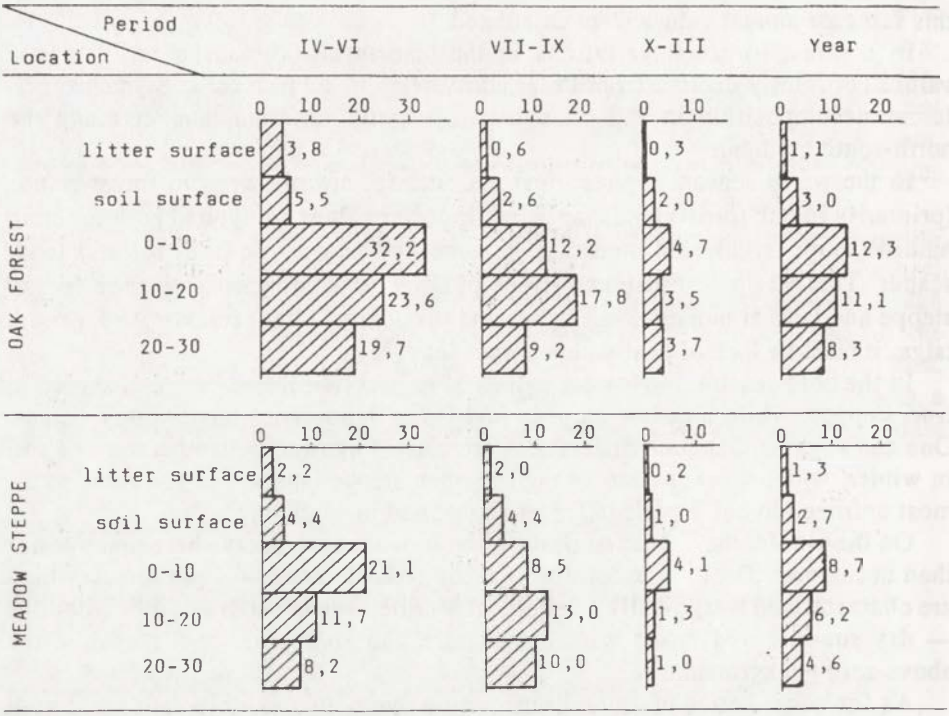

Fig.19. Seasonal rate of cellulose decomposition in the ecosystems of the Central Forest-steppe (%, mean in a month)

Thus, the presented materials clearly suggest that there exists a certain similarity in the way the principal hydrothermal factors affect both the productional and destructional processes in North Eurasian landscapes. As for differences, they are attributed firstly to the climatic impact affecting destruction in a more indirect way as compared with production, and, secondly, to the fact that the analyzed values characterizing destruction are qualitatively different. While the mortmass/production ratio depicts the process of destruction in an integral way, the destruction of cellulose applies only to that portion of total destruction which depends on the activity of microorganisms.

Now it is time to return to the problem of relationship between the role of biotic and abiotic factors in destruction. It is well-known that ecologists stick to the idea of the predominating role of bionts in all destructional processes. However, some of our experiments (Zlotin 1979; Zlotin, Khodashova 1980), while supporting the phenomenon of biological decomposition of organic matter, also

highlight the substantial role of abiotic factors, solar radiation in particular, in the decomposition of dead organic mass (Table 5).

Table 5. Rate of decomposition of litter fall (aspen and cereals, May-September) in field experiments with selective screens, meadow-steppe zone (after Zlotin, 1979)

Treatments / Decomposition measure	Control	Light screens			
		blue	colourless (polyeth. film)	red	sheet of plywood (full shade)
Grasses: dead leaves, initial weight 8 g					
Left by the end of exposition, g	6.04± 0.06	6.22 ± 0.03	6.34± 0.02	6.45 ± 0.05	6.50± 0.03
Decomposed, % of initial weight	13.7	11.1	9.4	7.9	7.1
Decomposed, % of the control	100	81	69	57	52
Aspen: dead leaves, initial weight 5 g					
Left by the end of exposition, g	3.49± 0.04	3.95± 0.02	4.05 ± 0.05	4.25± 0.03	4.29 ± 0.03
Decomposed, % of initial weight	30.2	21.0	19.0	15.0	14.2
Decomposed, % of control	100	70	62	50	47

The experiments were conducted in meadow steppes of the Central Chernozem Biosphere Reserve in Kursk region, 500 km south of Moscow. Fallen alder leaves and above-ground parts of steppe cereals were placed in containers with open tops for rain and sunlight. The experiment was repeated 4 times, with five degrees of light intensity controlled by special screens. Three screens were made of transparent synthetic polymers of various colours, while the fourth was made of a thin sheet of plywood impermeable to direct sunlight. The fifth (control) container had no screen.

The first blue screen let through about 80% of rays in the short-wave part of solar spectrum (shorten than 600 nm), but retained about 70% of thermal long-wave radiation. The red screen let through about 85% of long-wave radiation and retained 80% of short-wave radiation. The third, colourless screen made of a polyethylene film had no selective properties, but weakened all solar radiation flow by 50% as compared to the control variant. The fourth, plywood screen provided total shading from direct solar radiation. These conditions were maintained throughout the entire growing season, from May till September, by changing the angle of inclination of the screens and their sizes to reflect seasonal variations in sun elevation.

Results presented in Table 5 show that the degree of decomposition of the litter fall gradually declines with decrease of solar radiation intensity and decreasing of short waves part of its spectrum. Thus, only 47-52% of exposed leaves decomposed under the plywood screen with complete shading, as compared with the control sample. The other figures are: 50-57% under the red screen, 62-69%

under the neutral polyethylene screen and 70-81% under the blue screen. The reliability of this differences is rather high (P=0.01) for all variants, except of "polyethylene-red" and "red-plywood". Thus, the rays from the short-wave part of the solar spectrum are most effective in terms of destruction. The shading of plant fall nearly halves the rate of decomposition.

Field experiments with complete shading of litter fall by plywood screens were reproduced in true steppe, 700 km south of Moscow (50°N, 36°E) and in subtropical xerophytic pistachio forests (the State Badkhyz Reserve, 35°N, 62°E). The results received there also support the great role of direct solar radiation in the decomposition of above-ground plant fall (Zlotin 1979).

Field experiments on decomposition of different parts of litter and roots (Zlotin 1975, 1979) conducted in the warm and cold seasons allowed us to assess the role of various natural factors in the decomposition of total annual plant fall (Table 6): in an oak forest the share of abiotic factors is 15%, the share of microorganisms — 45%, invertebrates — 40%; in meadow steppe — 30, 55 and 15 %, respectively. Thus, the ratio of the four factors driving decomposition: 1) macrofauna, 2) mesofauna, 3) microorganisms, 4) abiotic factors can be presented as 6:1:1:2 in the oak-forest ecosystem and 1:1:1:7 in the meadow-steppe ecosystem.

Table 6. Rate of decomposition of dead plant parts (%) in two ecosystems of forest-steppe zone (Central-Chernozem Biosphere Reserve). Various acting factors, litter fractions and seasons were differentiated

Factors	Oak forest	Meadow steppe
Warm season		
Above-ground plant fall (green parts)		
Abiotic	14	72
Biotic		
microorganisms	10	11
mesofauna	30	9
macrofauna	46	8
Below-ground dead plant parts (roots)		
Abiotic	about 5	about 3
Biotic		
microorganisms	86	83
mesofauna	3	9
macrofauna	6	5
Whole year		
Total plant fall (above and below-ground)		
Abiotic	15	30
Biotic		
microorganisms	45	55
invertebrates (meso- and macrofauna)	40	15

MAJOR CONCLUSIONS

1. Along with the well-known latitudinal (north-south) gradient of different productivity parameters, there also exists a meridional (west-east) gradient in Northern Eurasia, which is mostly pronouced in the distribution of mortmass reserves and the values of the mortmass/annual productivity ratio.

The former is in good agreement with the zonal landscape differentiation, while the latter reflects its sectoral features, such as low precipitation totals and extremely low temperature of air and soil in winter.

2. Intersectoral (west-east) variations of productivity in forest and open landscapes are often in contrast. Thus, in Central Siberia, as compared with other sectors, phytomass and annual production in forests decline, while growing in tundras and steppes.

3. The role of well-known hydro-thermal boundary which roughly follows the southern boundary of the forest-steppe zone and separates humid landscapes from semi-arid landscapes is fairly well manifested in the spacial distribution of both, the productional and destructional parameters. Meridional gradients of nearly all productivity parameters are most pronounced to the north of this boundary, while latitudinal gradients are most pronounced to the south of it. Besides, the overall gradients in the fields of these parameters are much higher to the south of the forest-steppe and lower to the north of it.

4. In arid landscapes, interzonal i.e. climate-induced variations of productivity are less important than edaphic differences (for instance, between clay and sandy deserts) within a zone.

5. In humid landscapes, temperature predetermines difference in productivity both, between landscapes of different zones, and between north-and south- facing mesorelief slopes within one zone. The contrast between productivity indices on opposite slopes is highest in the tundra and forest-tundra zones, it declines southwards, nearly disappearing in the forest-steppe zone, where the temperature factor no longer predetermines the level of primary production.

6. Productivity of taiga landscapes with different ediphicators reacts in a different way to changes in the same climatic factors. For instance, larch forests are most sensitive to changes of the temperature, while pine forests are least sensitive.

7. In steppes, semi-deserts and deserts, i.e. in semi-arid and arid landscapes, the mortmass/production ratio varies slightly and is hardly related to phytomass reserves and annual production. In humid forest landscapes the ratio varies within a wide range which indicate corresponding variability of the biological cycle. Thus, this ratio is low in the warmest and most productive broad-leaved forests and highest in the coldest and least productive larch forests.

8. The rate of microbiological destruction of organic matter assessed through the rate of destruction of cellulose in soil is highest in oak - forest ecosystems of the forest-steppe zone and declines northwards and southwards, reaching its min-

imum in Arctic tundras and southern (subtropical) deserts. Thus, forest landscapes generally have higher destruction indices than open landscapes.

9. The intensity of destruction processes, like that of production processes, depends on the combination of heat and moisture availability. The low intensity of organic matter destruction in Northern ecosystems is caused by lack of heat, while in arid ecosystems — by lack of moisture. At the same time, one can observe certain geographical features in the proportion of destructional factors, namely, increased share of organic matter decomposed under the impact of short-wave solar radiation in open landscapes, as compared with the preferentially zoo-microbiological destruction in humid forest landscapes.

INFERENCE. A few words about tasks for the future. We consider it to be important to develop global and regional geographical analysis of production-destruction processes. It is important to distinguish regions in which productivity is regulated by specific combinations of environmental factors. Hierarchy of these factors should be fixed. It is necessary to reveal such territories, different in type and rate of ecosystems response to the same changes of environmental factors. At the same time, research not only of spatial connection between production — destruction processes and climate (or other parameters) but also their dynamics due to long data is required. Specific features of mountain and intrazonal landscapes should be analysed in detail.

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LITTER MASS LOSS IN PINE FORESTS OF EUROPE: RELATIONSHIPS WITH CLIMATE AND LITTER QUALITY

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Abstract. Decomposition of pine litter was studied in network of 37 sites (32 in Europe, 5 in US); climatic conditions were described as North European, Central European, Atlantic and Mediterranean. The effects of substrate quality and climate on decomposition were analysed. AET is the leading climatic constrain on mass loss rate (66 percent of variability of decomposition can be explained by climatic factors); for 11 selected sites over 90% in mass loss rates can be explained by litter quality variables, mainly nitrogen and phosphorous.

Key words: decomposition network studies, climatic constrains, litter quality

INTRODUCTION

F.G. Tenney and S.A. Waksman (1929) postulated that decomposition rates of soil organic matter are controlled by four distinct factors: 1) the chemical composition of the substrate, 2) a sufficient supply of nitrogen for the decomposer organisms, 3) the nature of the microorganisms involved, and 4) environmental conditions, especially aeration, moisture supply, pH and temperature.

At a given site and climate, one should expect mass-loss rates by a litter species to be related primarily to its chemical and physical properties. Indeed many studies have demonstrated such relationships (e.g. Upadhyay and Singh 1985, McClaugherty et al. 1985, Fogel and Cromack 1977, Aber and Melillo 1982, and Dyer 1986). As the decay of litter progresses through time, the constituents which regulate mass loss rates can change. A schematic model of these litter decay stages was presented by B. Berg and T.H. Staaf (1980). The early stages are regulated primarily by nitrogen and phosphorus concentrations whereas lignin concentration exerts the dominant control in the latter stages.

Climate, especially the heat and moisture delivery to the litter is no doubt a control of the rate at which the decay phases postulated by B. Berg and H. Staaf (1980) can proceed. Thus in one climatic regime the early, nutrient controlled phase

could persist while in other regimes this phase could be quickly passed (Dyer et al. 1990).

Because analyses of decay dynamics have been conducted using widely different litter types, and at sites in different climatic regimes and in different forest types, control by climate *versus* litter quality controls can confound our understanding. At broad regional scales the observed spatial patterns of mass-loss rates "appear" to be dominated by climatic variables, whereas litter properties appear to be relatively insensitive indicators of these macroscale patterns (Meentemeyer 1984). When the analysis is confined, however, to one or a few sites with similar climates, the influence of litter quality becomes apparent. With the recent increasing emphasis on understanding the impact of climate changes, climatic models and broad scale patterns of biological processes, the issues of model sensitivity and geographic scale become critical.

It is the primary purpose of this study to investigate for Western and Central Europe (and a few sites in eastern USA) the regional relationships between mass-loss rates and (i) climate, and (ii) initial litter concentrations of nitrogen, phosphorus and water soluble substances. These relationships will be examined using data from 37 sites of which 32 sites were located in Europe and 5 in the eastern part of the United States. At all sites a unified (or standard) needle litter was incubated in pine forests of different species. Also a set of experimental litters of different substrate qualities was incubated at selected Scots pine sites in northern Europe. The experimental design was nearly identical at all sites. A secondary purpose involves the creation of regional subsets of data from the 37 sites to identify differences in mass-loss dynamics that are not readily explained by the climatic and litter quality variables used in this study. The sites are to be divided into North-European, Central-European, "Atlantic" climate and Mediterranean climate sites. Finally these sites will be compared to identify unique regional responses in decay processes.

EXPERIMENTAL SITES

All experimental sites for the incubation of litter in litter bags were pine forests. Figure 1 gives the approximate location of the sites and Table 1 presents summarized information on the sites including geographic location and elevation, mean temperature and precipitation and pine forest type. Most of the sites in our investigation were Scots pine monocultures. Exceptions include Stone pine, Maritime pine, Radiata pine, Austrian pine and Corsican pine, which were used in Europe and sites with Red pine and Loblolly pine in North America, for a total of 8 different pine forest species. In all, 37 different sites spanning subarctic to subtropical and Mediterranean climates are represented. This is perhaps the largest network of directly comparable experimental sites ever devised for the study of biogeochemical processes. Descriptions of each site are provided in Appendix I, as well as references for more complete site descriptions.

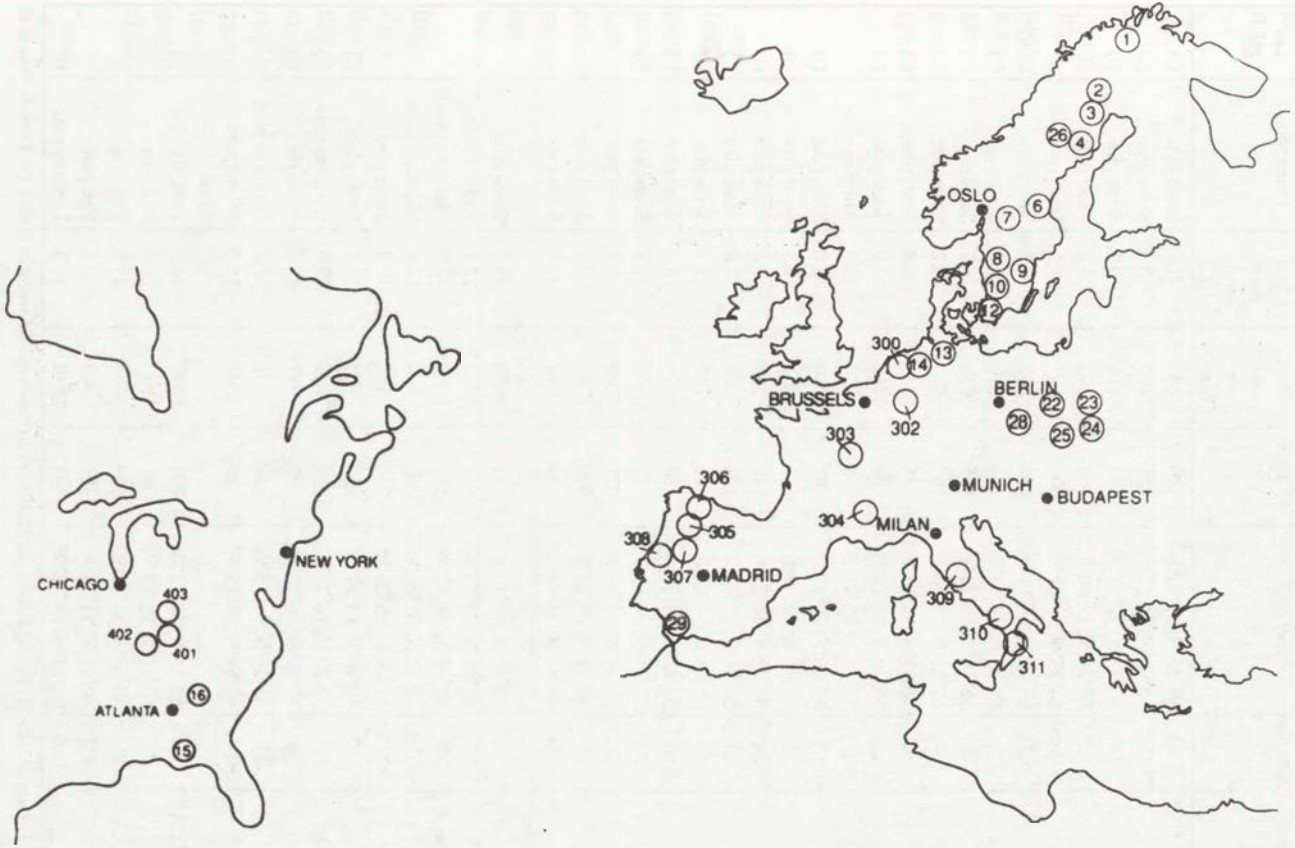


Fig 1. Approximate locations of experimental sites. Identification of site numbers and summarized site information are provided in Table 1. Appendix I provides additional, more complete site descriptions.

Table 1. List of sites used in this investigation, their geographic location and some site data

Site name	Site No	Lat/long	Altitude (m)	Ann mean prec. (mm)	Ann mean temp. (°C)	Pine species	Lit. ref.
Kevo	1	69°45'N; 27°01'E	90	443	-1.7	Scots pine	(1)
Harads	2	66°08'N; 20°53'E	58	470	0.6	Scots pine	(1)
Manjärv	3:1	65°47'N; 20°37'E	135	516	0.2	Scots pine	(1)
Norrliden	4:23	64°21'N; 19°46'E	260	595	1.2	Scots pine	(1, 3)
Granö	26	64°19'N; 19°02'E	300	527	1.5	Scots pine	(2)
Jädraås	6:51	60°49'N; 16°01'E	185	609	3.8	Scots pine	(1, 4)
Brattforsheden	7	59°38'N; 14°58'E	178	850	5.2	Scots pine	(1)
Nennesmo	8	58°16'N; 13°35'E	155	930	6.2	Scots pine	(1)
Mälilla	9	57°25'N; 15°40'E	105	670	6.2	Scots pine	(1)
Mästocka	10:1	56°35'N; 13°15'E	135	1070	6.8	Scots pine	(1)
Vomb	12	55°39'N; 13°19'E	46	770	7.0	Scots pine	(1)
Roggebotzand	300	52°34'N; 05°47'E	-5	826	10.3	Austrian pine	
Ehrhorn	13	53°00'N; 09°57'E	81	730	8.0	Scots pine	(1)
Czerlonka	23	52°41'N; 23°47'E	165	594	5.7	Scots pine	(1)
Mierzwice	24	52°20'N; 22°59'E	142	569	7.2	Scots pine	(1)
Pińczów	25	50°31'N; 20°38'E	191	689	7.6	Scots pine	(1)
Ede	14	52°02'N; 05°42'E	45	765	9.3	Scots pine	(1)
Olobok	28	52°22'N; 14°36'E	60	604	8.1	Scots pine	(1)
Wilków	22	52°24'N; 20°33'E	74	500	7.8	Scots pine	(1)
La Gileppe	302	50°34'N; 05°59'E	370	1200	6.9	Scots pine	
La Viale	304	44°11'N; 03°24'E	920	793	8.2	Scots pine	
Bois de la Commanderie	303	48°17'N; 02°41'E	83	677	11.0	Scots pine	
Albarese	309	42°40'N; 11°10'E	11	650	15.0	Stone pine,	
Capelada	305	43°40'N; 07°58'W	447	1062	12.9	Radiata pine	
Aguas Santas	306	42°44'N; 08°45'W	530	1500	12.5	Maritime pine	
El Raso	307:1	41°47'N; 05°26'W	760	402	12.4	Maritime pine	
El Raso	307:2	41°47'N; 05°26'W	760	402	12.4	Stone pine	
Terzigno	310	40°49'N; 14°29'E	250	960	13.2	Stone pine	(5)
Golia Forest	311	39°20'N; 16°27'E	1210	1225	9.0	Corsican pine	(5)
Doñana	29	37°07'N; 06°12'W	2	557	16.6	Stone pine	(1)
Furadouro	308:1	43°58'N; 09°15'W	80	607	15.2	Maritime pine	
Furadouro	308:2	43°58'N; 09°15'W	80	607	15.2	Mixed pine forest*	
Athens in USA	16	33°53'N; 83°22'W	207	1049	16.5	Loblolly pine	(1)
Mohican	401	40°36'N; 82°17'W	390	970	10.3	Red pine	
Blue Rock	402	39°36'N; 81°51'W	275	990	11.9	Red pine	
Ball's	403	40°41'N; 81°18'W	300	960	9.7	Red pine	
Tifton	15:2	31°28'N; 83°32'W	101	1540	19.3	Loblolly pine	(1)

(1) Breg et al. (1991); (2) Berg (1990); (3) Bååth et al. (1980); (4) Axelsson and Brikenhielm (1980); (5) Virzo de Santo et al. (in manuscript)

* 50% Radiata pine, 50% Maritime pine

Some *a priori* restrictions were applied to the site characteristics before the start of the decomposition measurements to insure plots with as much uniformity as possible. All sites were located on flat ground, and for most of the sites on nutrient-poor sediment soil. Care was taken to select sites with either none or very low understory. The sizes of the experimental plots varied but all of them had a minimum size to account for local conditions, e.g. canopy covers. Thus plot # 6:51 had an area of 100 m × 300 m. The other plots measured at least 50 m × 50 m, or, if irregular in shape covering a corresponding area (2500 m^2).

Even if there were some obvious differences in the sites' regional soils and landuse history, care was taken to select nutrient poor sandy sites. For the sites north of the Alps and the Carpatians the sites were on sandy sediment soils. The more northern sites had well developed litter and humus layers; however, some sites in the south had virtually no organic layer (e.g. El Raso and Terzigno). As a contrast, some sites (Capelada and Aguas Santas) had very thick organic layers (about 1 to 1.5 m).

MATERIALS AND METHODS

To meet the goals of this study, data were collected from 37 sites in 8 different types of pine forests which span a large range of climatic regimes. The experimental design was almost identical at all sites. Litter bag and litter sample preparation and handling procedures were standardized and conducted in one laboratory as well as all subsequent analyses. For each litter sample the initial concentrations of nitrogen, phosphorus, and water-soluble substances were measured. The concentrations of these nutrients and of water soluble substances have been shown to be good indicators of decomposition rates in early *versus* latter stages of decay (Berg et al. 1987; McClaugherty and Berg 1987).

Several studies have attempted to evaluate litter mass-loss data from litterbags as compared to other methods (Witkamp and Olson 1963; Lousier and Parkinson 1976; Johansson 1986). S.N. Rogers (1986) has shown that fractional decay constants based on litter-bag observations overestimate the decay rates of the entire litter layer because this layer includes much material in advanced stages of decay. This overestimation is, apparently, constant from one climatic regime to another. Measurements made by the litterbag method cover relatively early stages of litter decomposition in which the mass-loss rates are higher than in the more recalcitrant humus layers. Extrapolation to late stages of decay may not be possible but the measurements are clearly useful in the search for a climatic signal in decay dynamics.

Two main kinds of litter have been used in the present investigation, namely a "unified" Scots pine needle litter and different sets of experimental needle litter.

THE LITTER SAMPLES

Unified needle litter; The Scots pine needle litter was collected at the Jädraås site (the old site of the Swedish Coniferous Forest Project in east central Sweden) in early September from the branches of trees in a stand that was about 15 years old in 1973 when samples were first collected. The trees sampled were located within an area of about 100 m × 100 m. Annual variation in the quality of this litter is shown in Table 2.

Table 2. Annual variation in organic and inorganic chemical composition of Scots pine *(P. silvestris)* needle litter. Needle litter was collected at the time of needle abscission in September of each year (at a stand about 15 years old in 1973). Standard deviation within parenthesis. Part of the data are from B. Berg (1986)

Sampling (yr)	Concentration (mg · g^{-1})										
	Solubles		Lignin	N	P	S	Ca	K	Mg	Mn	Ash
	water	ethanol									
1973[1]	92	120	223	3.8	0.19	0.42	6.5	0.73	0.38	1.55	23
1974	145	84	276	4.2	0.22	0.29	5.4	0.71	0.49	n.d.	24
1975	172	107	238	3.4	0.20	0.32	4.7	0.61	0.39	n.d.	19
1976	151	89	255	4.0	0.21	0.36	4.9	0.53	0.42	n.d.	n.d.
1977	202	102	224	4.1	0.19	0.38	6.0	0.87	0.42	1.02	n.d.
1978	164	96	257	3.8	0.21	0.33	5.5	0.62	0.55	1.00	20
1979	129	95	288	10.4	0.29	0.78	2.3	0.97	0.39	0.31	12
1980	180	102	246	3.8	0.18	0.50	6.1	1.72	0.53	0.77	17
1981	213	94	231	3.9	0.28	0.61	7.1	1.02	0.58	1.17	23
1982	164	113	231	4.8	0.33	0.55	4.4	1.07	0.49	0.79	19
1983	178	112	229	3.8	0.30	0.45	5.9	0.90	0.39	1.08	26
1984	82	116	288	3.7	0.21	0.47	6.3	0.82	0.44	1.12	22
1985	182	94	241	2.9	0.19	0.45	4.8	0.52	0.38	1.24	18
1986	170	89	257	4.0	0.23	0.44	5.6	0.58	0.57	1.13	20
1987	162	100	250	3.8	0.21	0.42	4.9	0.55	0.41	1.18	18
1988	165	94	247	3.8	0.21	0.39	5.0	0.67	0.38	1.18	19
1989	n.d.	n.d.	n.d.	3.6	0.17	0.38	4.0	0.59	0.42	0.92	n.d.

Experimental needle litter; The needle litter from fertilized Scots pine stands was collected at the site of an optimum nutrition experiment at Lisselbo (Tamm et al. 1974). Litters from this site have been described earlier by B. Berg and H. Staaf (1980). The natural brown and green needle litter also was collected at the Jädraås site and brown Lodgepole pine needle litter was collected at a Lodgepole pine forest described by B. Berg and J.E. Lundmark (1987). The chemical composition of this litter is shown in Table 3.

Table 3. Chemical composition of four experimental Scots pine and Lodgepole pine needle litters incubated at sites numbered 1-14

Litter type	Concentration (mg · g^{-1})									
	water solubles	ethanol solubles	lignin	N	P	S	Mg	Ca	Mn	K
Scots pine										
— brown natural	164.2	112.6	231.4	4.8	0.33	0.55	0.49	4.42	0.79	1.07
— brown fertilized	134.9	91.4	264.9	7.0	0.33	n.d.	0.37	2.5	0.70	1.02
— green natural	198.6	63.3	284.2	13.4	1.47	0.98	0.85	2.82	0.41	4.90
Lodgepole pine										
— brown natural	102.5	41.7	380.5	3.9	0.34	0.62	0.95	6.35	0.95	0.56

Brown needles from the current generation of needles to be shed, were abscissed from the trees by shaking their limbs. After collection the litter was dried at room temperature and stored until sample preparation. The experimental green Scots pine needles were picked from the branches and were selected to be third year generation (C+2) needles.

The dry mass of the litter to be placed into litterbags was determined on 25 samples at 85°C. The largest difference in moisture content among samples was less than ± 0.5 percent of the average.

Litter-bags, (8 cm × 8 cm) were made of terylene net with a mesh size of about 1 mm. For each type of litter, 0.6-1.0 g of needles was placed in separate litter bags. At each site the bags were placed on the litter (L) layer in a measurement plot (1 m × 1 m) in each of 25 "spots" in a randomized design within a larger plot. Bags were fastened to the ground by 10-15 cm long metal pegs; a new placement of bags for incubation was made whenever retrieval of samples was made. Retrieval of litter bags took place between once to six times annually. At a given site on each occasion one litter bag of each litter type was collected from each of the 25 spots.

LABORATORY ANALYSES

DETERMINATION OF MASS-LOSS

After collection and drying at a laboratory near each site, the 25 litter bag samples of each type were sent to one common laboratory and cleaned. Plant remains, such as mosses, grass and shrub materials were removed. The loss of dry mass was then determined by drying the samples to a constant mass at 85°C. Mean values of mass loss were calculated for each sample set of 25 bags.

CHEMICAL ANALYSES

Chemical analyses were carried out on the fresh, initial litter samples only. The samples were ground in a laboratory mill equipped with a filter allowing par-

ticles of less than 1 mm to pass. The amounts of water-soluble and ethanol soluble substances were determined by sonicating the milled samples three times in a sonicator bath and weighing the samples after filtration and drying. The analysis for sulfuric-acid lignin and soluble substances in the needle litter were carried out according to P.O. Bethge et al. (1971)(see also Berg et al., 1982). The milled samples were further analyzed for total contents of the elements nitrogen, phosphorus, sulfur, potassium, calcium, magnesium, manganese, and total ash.

Elemental nitrogen was determined by combustion (Elemental Analyzer NA 1500; Carlo Erba, Strumentazione, 20090 Rodano, Milan, Italy). For the analysis of phosphorus, magnesium, potassium, calcium and manganese, samples were digested for 2 days in a 2.5:1 (v/v) mixture of nitric and perchloric acid. The analyses were performed by plasma atomic emission spectrometry ICP-AES (Jobin YVON JY-70 Plus 16-18, rue du Canal 91163, Longjumeau, France). Ash concentration was determined by combustion at 550°C for 2h.

CHEMICAL COMPOSITION OF LITTER TYPES

All of the unified Scots pine needle litter was collected at one location at the Jädraås site. Collections were made annually and the chemical composition varied somewhat among years (cf Berg 1986). The chemical composition of the litter preparations used in this study are given in Table 2.

INCUBATIONS OF DIFFERENT COMBINATIONS OF LITTER TYPES

The unified litter was incubated either annually, twice or three times a year at the different sites. Although the litter originated from the same site there were some differences in chemical composition among years. The nitrogen concentration ranged from 4.8 to 2.9, phosphorus from 0.33 to 0.19. Sulfur varied from 0.21 to 0.61 and calcium from 7.1 to 4.4 $mg \cdot g^{-1}$. Ash concentrations were comparatively low going from about 20 to 26 $mg \cdot g^{-1}$. Also the more mobile ions, including K and Mn had a variation of the same magnitude as phosphorus; concentrations ranged from 1.02 to 0.52 and 1.55 to 0.79 $mg \cdot g^{-1}$ respectively.

Of the **experimental litters**, one set of four different litters was incubated at 11 sites in northern Europe (cf Table 4). For the site 6:51 (Jädraås) additional data sets used in previous studies were also available. Thus for the Jädraås site 10 additional observations could be taken from a paper by B. Berg and H. Staaf (1980) and four values from B. Berg and G. Ekbohm (1991).

CLIMATIC DATA

For some of the experimental sites the collaborating authors provided excellent site descriptions as well as some summarized weather data. These data were

used whenever possible to assist in the calculation of a suite of climatic and water balance variables. For most of the sites the monthly temperature and precipitation had to be estimated on the basis of data from surrounding weather stations. For all of the sites long term, average climatic data were based on world climatic data records collected by C.J. Willmott et al., (1981 a, b). In addition to interpolation among surrounding stations, adjustments were also made for the site's elevation. The climatic data were in turn used to calculate the water balance variables of each site based on the procedures of C.W. Thornthwaite and J.R. Mather (1957). A computer program (WATERBUD) designed by D.M. Sharpe and C.W. Prowse (1983) was used to calculate monthly and annual values of potential evapotranspiration (PET), actual evapotranspiration (AET), soil moisture deficit (DEF) and soil moisture surplus (SUR). For each site a soil moisture storage value of 300 mm was assumed for the root zone to make the results of the present study comparable with previous work (e.g. Meentemeyer 1978, 1984; Meentemeyer and Berg 1986; Dyer et al. 1990). The temperature, precipitation, and water budget and litter quality variables used in this study, as well as a short code used for each variable, are presented in Table 4.

Table 4. List of variables and their computer codes

LOSS	Mass loss in the first-year of decomposition (%)
NITR	Initial nitrogen concentration (mg · g^{-1})
PHOS	Initial phosphorus concentration (mg Ã γ^{-1})
WSOL	Initial water solubles concentration (mg · g^{-1})
JULT	Average temperature for July (°C)
AVGT	Average annual temperature (°C)
RNG	Annual temperature range (°C)
PRECIP	Total annual precipitation (mm)
PRANGE	Annual precipitation range (mm)
PET	Potential evapotranspiration (mm)
AET	Actual evapotranspiration (mm)
SUR	Soil moisture surplus (mm)
DEF	Soil moisture deficit (mm)

RESULTS AND DISCUSSION

All needle litters were incubated in regions with AET ranging from more than 300 to less than 1000 mm and all sites had a first-year mass-loss of less than 56 percent.

The sites representing the entire data set had differing numbers of observations, ranging from 19 1st-year mass-loss values for site 6:51 (Jädraås) to just one for ten sites. Some of the sites with only one observation have just recently started operation. Because long-term climatic average values were used, the average for mass-loss, and the substrate quality variables were used for the sites that had more than one year of observation. Even before statistical analyses were

started, patterns based on the regional origin of data were apparent. This suggested that separate analyses of subsets of the data could provide additional information.

As the unified litter had some variation in chemical composition among years, we selected for analysis those incubations at each site that had litter with identical chemical composition. Thus the litter collected in 1985 had been incubated at 18 sites, the litter collected in 1984 at 16 sites and the litter collected in 1982 incubated at 12 sites. These sets were used for a special analysis of the effect of substrate quality on mass-loss rate.

ANALYSIS OF THE WHOLE DATA SET

In a first step to determine the degree of relationship among the climatic variables, litter quality variables and mass-loss rates, a correlation matrix was created using data from all 37 sites. Potential variables for use in a broad-scale climatic/litter quality model were selected based on degree of relationship and minimization of multicolinearity (cf Appendix II).

SIMPLE CORRELATION AND REGRESSION

All of the independent variables selected were individually plotted and regressed against annual mass-loss rates (LOSS) for the 37 sites to check for curvilinear relationships. None was found so the linear form was deemed adequate. Regression coefficients were then examined to narrow the list of potential explanatory variables.

Of the suite of climatic variables, the best correlations obtained using single variables were positive for the relationship between LOSS and actual evapotranspiration (AET), the total precipitation (PRECIP), and average temperature (AVGT) with R^2 values of 0.489, 0.316 and 0.192 respectively, all statistically significant at $p < 0.01$ (Table 5). Potential evapotranspiration (PET) gave a significant relation at the $p < 0.05$ level. Water deficit (DEF) also gave a significant relation even if barely so. This factor was considered of interest for regional comparisons since some sites clearly had high values for water deficit.

The best single variable (AET) was plotted against first year mass-loss and each site was located on the plot (Figure 2). The progression in rates from the subarctic (site # 1) to the subtropical (site # 15) is readily apparent. Some of the scatter in Figure 2 can be attributed to the use of long-term climatic normals rather than information about the weather during incubation. The Georgia sites (# 15 and 16) should be expected, for example, to have higher rates of mass-loss (than those shown) in normal years because incubation occurred in an extremely dry year. Some of the variation must also be caused by variations in litter quality and local site conditions. As will be seen later, stratification of the data sets can

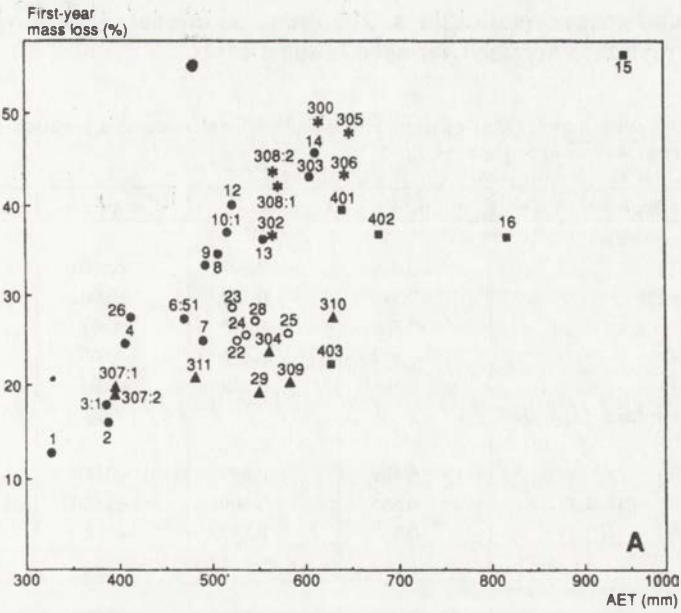
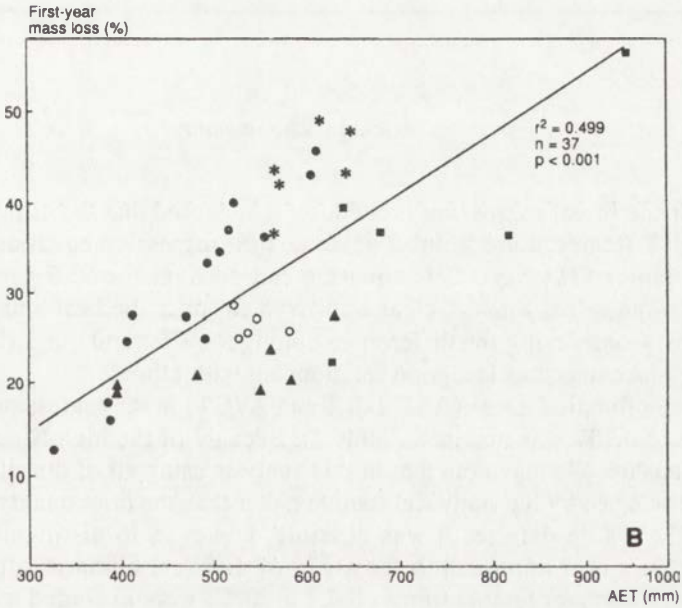


Fig. 2A. Bivariate plot of average first-year litter mass-loss *vs* actual annual evapotranspiration. All sites used, (n=37).



(•) Scots pine sites in an intensively studied Scandinavian-NW-continental transect ranging from northern Finland to central Holland; (*) pine sites close to the European west coast or sites relatively exposed to Atlantic climate; (▲) pine sites around the Mediterranean; (O) Central European Scots pine sites (Poland) with characteristics of inland climate; (■) pine sites in the eastern inland of the United States.
A. Site numbers identify the mass-loss values for each site

lead to much stronger relationships. The use of additional climatic variables can greatly improve the explained variance in some cases.

Table 5. Annual mass loss (LOSS) of litter at a broad regional scale as a function of some single climatic factors as well as multiple ones, (n=37)

Eq.	R^2	r	p	Comments
Single linear regression				
LOSS = f (AET)	0.489	0.699	<0.001	
LOSS = f (PRECIP)	0.316	0.562	<0.001	
LOSS = f (AVGT)	0.192	0.439	<0.01	
LOSS = f (PET)	0.172	0.415	<0.05	
LOSS = f (DEF)	0.108	-0.329	<0.05	
Stepwise multiple linear regression				
All sites (n=37)				
LOSS = f (AET)	0.489	0.699	<0.001	
LOSS = f (AET) + f (JULT)	0.665	0.809	<0.001	Jult gave a neg rel.
LOSS = f (AET) + f (JULT) + f (AVGT)	0.737	0.859	<0.001	
All sites with lower summer temperatures (n=28)				
LOSS = f (AET)	0.662	0.814	<0.001	
LOSS = f (AET) + f (PRECIP)	0.713	0.833	<0.001	
LOSS = f (AET) + f (PRECIP) + f (WSOL)	0.761	0.873	<0.001	

MULTIPLE VARIABLE RELATIONSHIPS

In a multiple linear regression procedure, it appeared that the climatic factors AET and JULT (temperature in July) gave the best regression equation using two climatic variables (Table 5). This equation can account for 66.5 percent of the variability in mass-loss rates, a clear improvement over the best single-variable relationships. Considering the differences among the sites and the different years of litter bag placement this is a good relationship with climate.

With three climatic factors (AET, JULT and AVGT) in the regression procedure an R^2 value of 0.737 was obtained (Table 5). Because of the high N size, this is a stable relationship. We may note that in this analysis using all of the sites, climatic factors were selected by the statistical routine rather than the litter quality variables.

Within the whole data set it was possible, however, to distinguish regional differences. In a first approach to the study of different climatic situations, the sites with high summer temperatures (JULT > 20°C) were excluded meaning that all North American sites and the low-altitude Mediterranean ones were left out giving 28 sites for analysis. As in the previous analyses the climatic factor AET was the leading variable with an R^2 value of 0.662. As a second factor the program selected annual precipitation (PRECIP) resulting in an R^2 value of 0.713. In this analysis a substrate

quality factor was included by the program as a third variable *viz.* water soluble substances (WSOL), resulting in an increase in the R^2 value to 0.761.

For the sites with JULT above 20°C a separate analysis was run using 11 sites. The best climatic variable was again AET with an R^2 value of 0.777. Water deficit (DEF) the next best variable gave a negative relationship with an R^2 of 0.372. JULT gave an R^2 of 0.369. This demonstrates again the power of AET as a predictor of mass loss rates. But it also shows that the mix of useful climatic variables can change with the region and its climatic regime. Because of the small sample size no further analyses using multiple variables were used.

ANALYSIS OF THE SCOTS PINE SITES

Special attention was given to the Scots pine sites because many of the sites in Europe represent this kind of ecosystem. The geographical range presented here covers almost the entire north-south range of this species in Europe; the northernmost site is in Northern Finland close to Barents Sea and the southernmost (La Viale) in Southern France. The sites also are relatively homogeneous with respect to thickness of the soil organic matter layer and ground vegetation.

In a special analysis for the Scots pine sites north of the Alps and the Carpatians (N=21), AET as a single variable gave a highly significant relationship (R^2=0.656). The addition of WSOL as a substrate quality index increased the R^2 value to 0.740, whereas the concentrations of N and P (NITR and PHOS) did not improve the fit. Within this group, the Polish sites could be seen to form a group with lower than expected mass-loss rates (Fig. 2; see the Central-European sites).

A special set of sites with numerous observations was investigated; a set of 13 sites in Scandinavia and the northwestern part of the continent. These sites had mass-loss measurements over a period which varied between 6 and 19 years. Of the single factors, AET gave a highly significant relationship with an R^2 value of 0.878. It is likely that the multiple years of observations caused an average calculated mass-loss rate more representative of the climatic norms used in this study. The addition of substrate quality factors such as WSOL, NITR, and PHOS did not improve the fit, probably because the variation in this set of litters was relatively small. At each of these sites, however, a special set of experimental litters was incubated (Table 3) which permitted an attempt to model the unique influence of litter quality in early decomposition stages.

THE EFFECT OF SUBSTRATE QUALITY ON MASS-LOSS RATES

At a particular site it has been shown that litter materials decay at rates dictated mostly by their chemical and physical properties. These relationships appear to be unique to the site and its decomposer organisms and prevailing

microclimate. Predictions of decay rates for other sites cannot therefore be made with confidence. Nevertheless the decay dynamics at a site must include the combined effects of both climate and litter quality variables. A separate analysis to produce models of this combined effect was performed.

Data from 11 sites, for which at least four litters of different properties were incubated were selected. These sites occur in Germany, The Netherlands, Sweden and Finland (Table 1). For each site the litter quality variables (nitrogen, phosphorus and water soluble constituents) were regressed against annual mass loss. Most of the regressions, even considering the small N-size at each site, were significant (at $p<0.1$). Examination of the alpha and beta coefficients for each regression equation at each of the 11 sites suggested a regularity in coefficients which is influenced by climate. This is in agreement with patterns in alpha and beta coefficients found by M.L. Dyer (1986). In earlier work. V. Meentemeyer (1978) demonstrated a geographically and climatically varying influence by lignin concentration on mass-loss rate.

A new data set of alpha (intercept) and beta (slope) coefficients for the 11 sites was devised and a second order regression analysis performed using each of the climatic variables to determine the degree to which the coefficients vary with climate. For both nitrogen and phosphorus the alpha coefficients for the sites were strongly and positively related to annual potential evapotranspiration (PET) and the beta coefficients were related to the site's precipitation (PRECIP). Thus the intercepts appear to be driven mostly by climatic heat and the slopes of the relationship (mass loss *versus* quality) by the gross water supply (PRECIP). The relationships using coefficients for water solubles (WSOL) were very weak and deemed inadequate for modelling purposes.

The "expanded" model for the influence of initial phosphorus concentration at any particular site may be written as:

$$\text{mass-loss}_{Phos} = (-29.3 + 0.111(PET))+(0.749+0.013(PRECIP))(PHOS) \quad (1)$$

where the first statement in parenthesis is in reality a new alpha coefficient determined by a site's PET (mm) and the second term is a new beta coefficient driven by annual precipitation (mm). The third term is the individual litter's phosphorus concentration.

For nitrogen control of mass-loss the expanded model may be written as:

$$\text{mass-loss}_{Nitr} =(127.3+0.100(PET))+(-0.067+0.0022)(PRECIP))(NITR) \quad (2)$$

where the first statement is again determined by site PET, the second by precipitation and the third by the litter's nitrogen concentration.

Figure 3 is a nomogram constructed from equation 1 (phosphorus). Selected PET values are shown on the left vertical axis, annual precipitation (PRECIP) on the horizontal axis and predicted mass-loss rates on the right vertical axis. The figure provides predicted loss rates for PET values of 400 mm and 600 mm, variable precipitation (from 200-650 mm) and initial phosphorus concentration of 0.15(a), 0.30(b), 0.60(c) and 1.20(d). Thus PET selects the intercept, precipita-

tion, the slope and initial phosphorus concentration then predicts the loss rate for a given site's PET and precipitation.

These relationships also suggest that most of the regional variation in loss rates across northern European Scots Pine forests is driven by temperature/heat constraints. As precipitation increases the differences in loss rates for litters of differing phosphorous concentrations became larger.

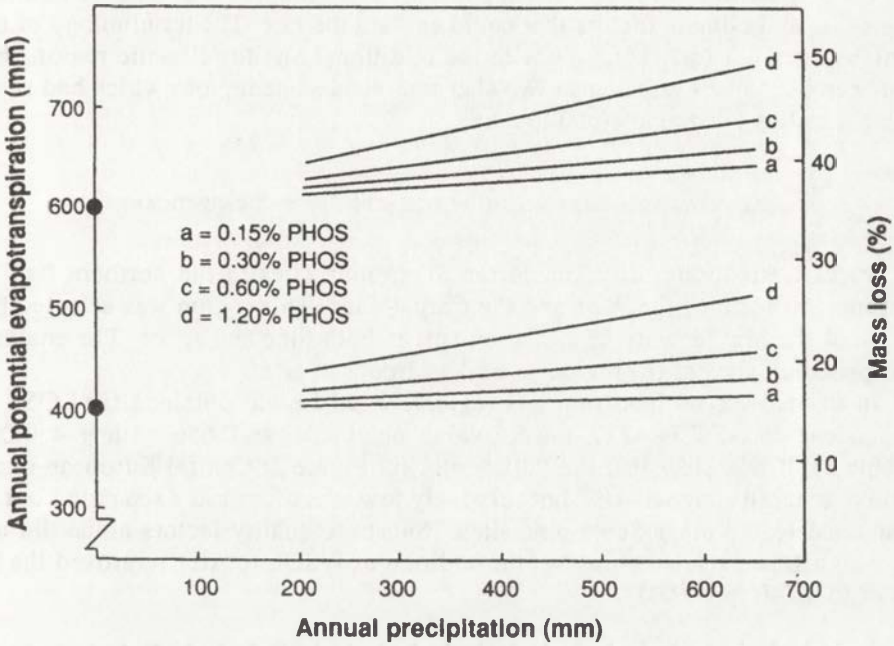


Fig. 3. Nomogram constructed from equation(1)

Selected PET values are shown on the left vertical axis, annual precipitation (PRECIP) on the horizontal axis and predicted mass-loss rates on the right vertical axis. The figure provides predicted loss rates for PET values of 400 mm (lower set of graphs) and 600 mm (upper set of graphs) and four initial phosphorus concentrations (PHOS) of 0.15 $mg \cdot g^{-1}$ (a), 0.30 $mg \cdot g^{-1}$ (b), 0.60 $mg \cdot g^{-1}$(c), and 1.20 $mg \cdot g^{-1}$ (d).

This figure shows in a different way our conclusion regarding climate *versus* litter quality influences drawn from analyses of observations of mass-loss rates covering large geographical areas. Even small changes in climate, can produce greater changes in early-stage decay rates than rather large differences in litter quality. Thus it should not be surprising that quality variables are important at local scales but their influences are "apparently" less significant when viewed at broad spatial scales. Nevertheless the equations presented here should permit predictions of the influence of litter quality across a broad area of Northern European pine forests, especially Scots pine forests.

REGIONS AND REGIONAL COMPARISONS

Within the whole data set it was possible to distinguish differences in mass loss patterns among regions, data sets that tended to deviate from the general AET model. Based on climatic data and the results from the analysis of the whole data set (cf Figure 2) we made an attempt to distinguish groups of sites at which the decomposition followed certain patterns. The grouping was based on annual mass loss and climate factors that could explain the rate. The terminology of the regions does not fully coincide with the traditional one for climatic regions but has been used in a looser sense. We also combined some regions which had some characteristics in common (cf Table 6).

ALL SCOTS PINE SITES NORTH OF THE ALPS AND THE CARPATHIANS

Special attention was given to the Scots pine sites in the northern half of Europe *viz.* north of the Alps and the Carpathians. This region was selected because of the high density of measurements in both time and space. The analysis comprised all sites of the region as well as groups of sites.

In an analysis of data from this region a good fit was obtained for LOSS as dependent on AET (N=21); the R^2 value obtained was 0.656 with $p < 0.001$ (Table 6). It was clear that the Polish sites (cf Figure 2; Central-European sites) with a generally higher AET but relatively low mass-loss rates separated out as compared to the other Scots pine sites. Substrate quality factors alone did not give significant relationships but the addition of WSOL to AET improved the R^2 value to 0.740 ($p< 0.001$).

ANALYSIS OF THE SCANDINAVIAN-NORTHWEST-EUROPEAN SITES

An analysis was conducted using data from a transect in which long-term studies had been carried out for at least about 10 years, thus giving good long-term average values for litter mass-loss. Using all 13 sites a regression using AET alone gave an R^2 value of 0.878 and $p < 0.001$. The addition of other climatic factors added very little to the explained variance. Substrate quality factors alone did not give any significant relationship but the inclusion of NITR or WSOL as a substrate quality index improved the relation somewhat; for NITR an R^2 value of 0.895 was obtained.

Part of this transect was placed in Scots pine standardized forests on flat ground and sediment soils. Thus it appeared that the "standard transect" of 10 Scots pine sites on sandy, nutrient-poor sites gave a fit to AET at nearly the same level as all the 13 sites (n=10; R^2=0.878; $p < 0.001$).

Table 6. Linear correlations and regressions between litter mass loss (LOSS) and selected climatic factors, as well as some substrate quality factors. Sites were grouped and labeled; groups were investigated separately as well as in combinations of groups

Eq.	R^2	p
Scots pine sites north of the Alps and the Carpathians (n=21)		
LOSS = f (AET)	0.656	<0.001
LOSS = (AET) + f (WSOL)	0.740	<0.001
Scandinavian-Northwest European sites (n=13)		
LOSS = f (AET)	0.878	<0.001
LOSS = f (AET) + f (NITR)	0.895	<0.001
Central European sites (n=5)		
LOSS = f (AET)	0.003	n.s.
LOSS = f (NITR)	0.045	n.s.
Atlantic sites (n = 7)		
LOSS = f (AET)	0.543	<0.1
LOSS = f (NITR)		n.s.
LOSS = f (AET) + f (NITR)	0.572	<0.1
LOSS = f (AET) + f (DEF)	0.566	<0.1
Mediterranean sites (n=7)		
LOSS = f (AET)	0.466	<0.1
LOSS = f (DEF)	0.511	<0.1
LOSS = f (JULT)	0.006	n.s.
LOSS = f (AET) + f (NITR)	0.509	n.s.
LOSS = f (AET) + f (DEF)	0.645	<0.05
North American sites (n=5)		
LOSS = f (AET)	0.650	<0.1
LOSS = f (NITR)	0.374	n.s.
LOSS = f (DEF)	0.000	n.s.
LOSS = f (JULT)	0.476	n.s.
LOSS = f (AET) + f (NITR)	0.803	n.s.
LOSS = f (AET) + f (JULT)	0.748	n.s.
Combinations of groups of sites		
Scandinavian-NW-European plus Atlantic sites (n=20)		
LOSS = f (AET)	0.913	<0.001
LOSS = f (NITR)	0.055	n.s.
LOSS = f (AET) + f (NITR)	0.915	<0.001
Mediterranean sites plus Central European ones plus North American sites (n=17)		
LOSS = f (AET)	0.753	<0.001
LOSS = f (NITR)	0.063	n.s.
LOSS = f (AET) + f (NITR)	0.057	<0.001
LOSS = f (AET) + f (DEF)	0.766	<0.001
LOSS = f (AET) + f (JULT)	0.761	<0.001

CENTRAL-EUROPEAN SITES

There were few European sites that would have a clear inland climate. The sites # 22-25 and 28, all in Poland seemed to have, however, the most pronounced continental climate. The range in mass loss as well as in AET was narrow (Figure 2) and it was not possible to find any significant relationships between LOSS and climatic or substrate quality factors. These loss rates appear slower than might be expected using all the sites as a comparison and the climatic variables selected for this study. They are, however, more similar to other inland sites in this study.

ATLANTIC SITES

Seven sites were located either very close to the European west coast or so close that they could be expected to be influenced by the Atlantic climate (please see * symbol in Figures 1 and 4A). This selection was, of course not unequivocal, and some alternative approaches were tested. When comparing litter mass loss to AET the R^2 value became 0.543 which was not significant ($p < 0.1$). No combinations with other climatic factors or litter quality improved this relationship (Table 6). There were five sites in the Scandinavian transect (*viz.* # 8, 10:1, 12, 13, and 14) that could be classified as being under Atlantic influence and in one approach these were included which improved the relation AET *vs* LOSS to reach the significance level of p.

MEDITERRANEAN SITES

The Mediterranean sites fell into two groups as it appeared that the decomposition was higher at four of them at comparable AET values, whereas seven of them had high water deficits for the summer months. The most characteristic Mediterranean sites *viz.* # 29, 304, 307, and 309-311 had clearly lower mass-loss rates than had the more Atlantic sites at the same latitude (# 305, 306, 308:1 and 308:2) (Figure 2). The high DEF apparently retarded the decomposition rates and AET alone did not give any significant relation to LOSS whereas a multiple linear regression with AET and DEF gave a better fit ($p < 0.05$)(Table 6).

NORTH AMERICAN SITES

Five sites (Figure 2) were situated in the inland of the Eastern United States. These sites had relatively high AET values whereas the measured mass-loss values were relatively low. A linear regression using these sites gave a weak relationship between LOSS and AET ($p < 0.1$; Table 6) whereas attempts to include JULT and DEF gave nonsignificant results.

THE SCANDINAVIAN-NORTHWEST EUROPEAN SITES PLUS THOSE WITH ATLANTIC CLIMATE

The sites in the Scandinavian transect (n=13) and the sites with an Atlantic climate (n=7) had similar responses between LOSS and AET (Figure 2). They had low DEF with the exception of site # 308 that is, however, located very close to the coast. As they seemed to have similar responses an attempt was made to combine them for an analysis. Using all 20 values and comparing AET and LOSS gave a very good fit with an R^2 value of 0.913 (Table 6; Figure 4A). This relationship which explained 91 percent of the variance in the decomposition rates was not improved by the addition of other climatic factors or substrate quality.

SITES WITH DRY AND WARM SUMMER CLIMATE

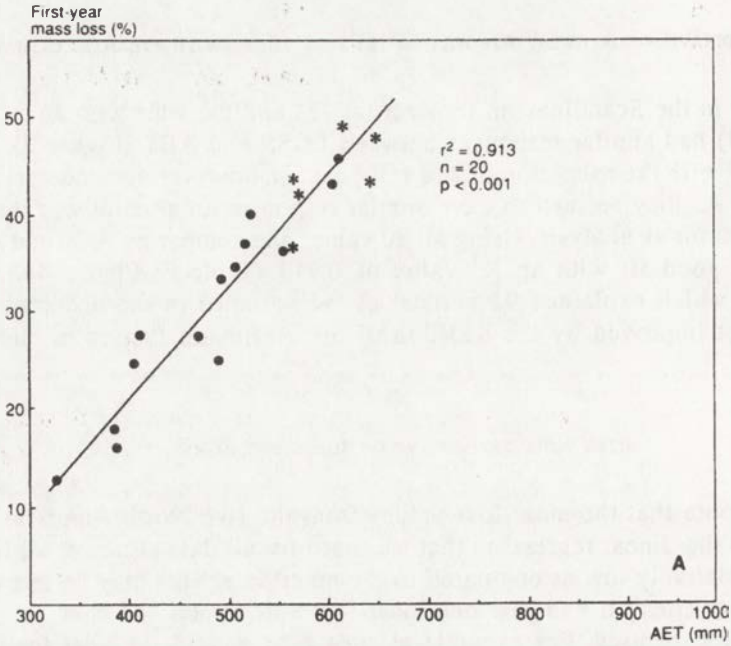
We may note that the mass-loss values from the five North American sites fitted well to the linear regression that was used for all data although all five of them were relatively low as compared to the other data. This may be due to the fact that these sites all had just one mass-loss value each and that long-term climatic data were used. For example at sites # 15 and 16 the year for which mass-loss was measured was extremely dry, thus giving very low values.

Mass-loss values for the sites characterized by dry and warm summers were combined into a linear regression encompassing sites called "Mediterranean", "Central European", and "North American" thus allowing us to investigate the effect of a main climate type on 17 sites on a broad geographical range.

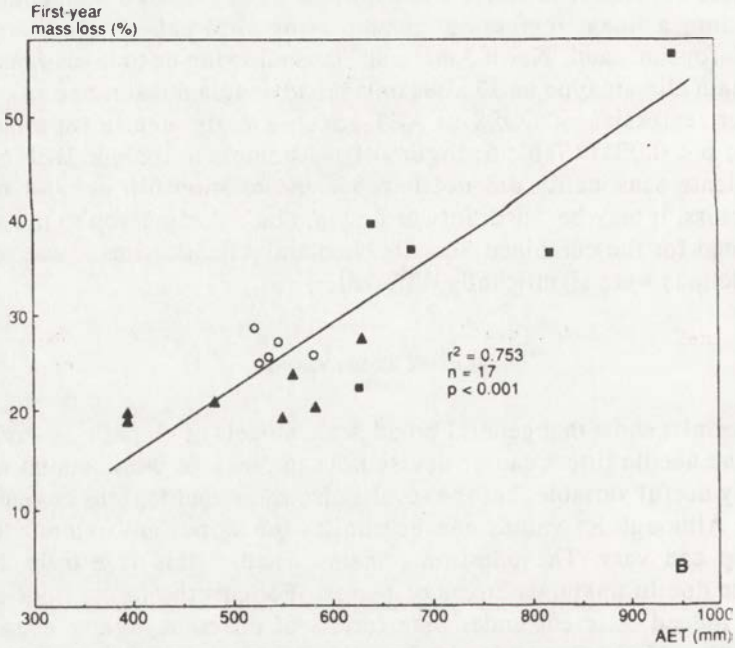
A linear regression of LOSS *vs* AET gave a clearly significant relationship (R^2=0.753; $p < 0.001$) (Table 6; Figure 4B). Attempts to include DEF or JULT, which indicate seasonality did not improve the relationship nor did substrate quality factors. It may be worth forwarding that on a comparison to the relationship obtained for the combined Scandinavian and Atlantic sites it was seen that the two relations were significantly different.

REGIONAL COMPARISONS

These results show that general broad-scale models of climatic control of loss rates of pine needle litters can be devised. As in previous work annual AET is a particularly useful variable, but the results also show that regions have differing responses. Although R^2 values can be similar the slopes and intercepts of the relationship can vary. The question remains whether this is a truly differing response or due to unknown errors or biases. Perhaps the forest floor environments are indeed different under pine forests of different regions even though macroclimatic AET values are similar. We included climatic variables which respond to seasonality and continentality, but none of these variables could help explain lower rates in Mediterranean and Inland sites. The mix of years and sites used suggest this is not an experimental error. Furthermore, the results using the



A. Scots pine sites in a Scandinavian-NW-continental transect and pine sites close to the European west coast or sites relatively exposed to Atlantic climate (n=20)



B. Mediterranean sites, central European ones and North American ones (n=17)

Fig. 4. Bivariate plot of average first-year litter mass-loss *vs* actual evapotranspiration. Denominations as in Fig. 2

ennoscandian and Atlantic sites are very similar to those found by V. Meenemeyer and B. Berg (1986) using earlier data sets for Fennoscandia and weather ecords for the actual incubation period. Regressions using AET versus LOSS ad alpha and beta coefficients and R^2 values similar to those found here. Other ariables must be in operation at more continental sites.

SUMMARY AND CONCLUSIONS

It was the purpose of this study to stress regional variation in litter mass-loss ates (first year) across a large, continental scale area, dominated by pine forests. his variation could be analyzed on the basis of 37 experimental sites spanning limatic regions from the subarctic to subtropical and Mediterranean: the atitudinal gradient ranged from 31°N to 70°N and may represent the largest eographical area that has ever been sampled and observed for the purpose of tudying biogeochemical processes. Because of stratification procedures and niform laboratory procedures, data from all sites are directly comparable. These rocedures also permitted a determination of the relative influence of climate *ersus* substrate quality viewed from the perspective of broad regional scales.

The observations of litter mass-loss, initial litter quality and a suite of limatic variables for each site permitted analyses of the entire data set as well as egional subsets. Tests of stratification procedures and litter quality permitted eparate analyses. Simple correlation-regression procedures applied to the entire lata set indicated that annual actual evapotranspiration (AET) should be the leading climatic constraint on mass-loss rates ($R^2 = 0.489$). The combination of AET, verage July temperature (JULT) and average annual temperature (AVGT) could xplain over 66 percent of the sites' variability on litter mass-loss. In an analysis f 21 Scots pine sites north of the Alps and Carpathians, AET alone could account for about 66 percent of the variation and the addition of a substrate quality ariable was sufficiently significant to be used in a model.

In an attempt to "force" the influence of litter quality into a model, data from 1 sites at which litters of different quality had been incubated was selected. hese sites are found in Germany, the Netherlands, Sweden and Finland. At any ne site most (≈ 90 percent) of the variation in mass-loss rates could be explained by one of the litter quality variables (NITR, PHOS, WSOL). These nodels are based on either NITR or PHOS, and PET and AET; they show that ven small changes in PET (and to a lesser degree precipitation) can result in arge changes in early-phase decay rates.

Further regional subdivision of the data set, resulted in a range of strength in he relationship between climatic variables, from very weak in Central Europe to trong for the Scandinavian and Atlantic coast sites ($R^2 = 0.913$, AET *versus* OSS). Much of the variation in observed loss rates could be related to continenal *versus* marine/Atlantic influences. "Inland" locations had mass-loss rates ower than should be expected on the basis of for example AET alone. Attempts

to include seasonality variables were not successful. It is clear that either unknown errors and biases, or, unknown variables are causing these regional differences in response to climatic variables. Nevertheless these results show the powerful influence of climate as a control of the broad-scale geography of mass-loss rates and substrate quality at the stand level.

Some of these relationships between mass-loss and climatic variables are among the highest ever reported, probably because of the care taken to select uniform sites and experimental methods. This suggest that superior, base line maps of predicted mass loss rates could be produced using climatic data. These models should be useful to predict the changing equilibrium litter dynamics resulting from climatic change.

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APPENDIX I.
Site Descriptions, including summarized climatic data and references for more complete descriptions

Site **Kevo (No 1)**, northernmost Finland in Kevo Natural Concervancy, about 120 km north of the town Ivalo, is located at 69°45'N; 27°01'E, at an altitude of 90 m. The average annual temperature is 2.4°C and average annual precipitation 420 mm. The stand has a Scots pine (*Pinus silvestris*) monoculture and a very low and sparse understory composed mainly of lichens. The soil is nutrient poor sandy sediment and the humus type is a mor.

Site **Harads (No 2)**, north Sweden, about 100 km north-west of the city Luleå is located at 66°08'N; 20°53'E at an altitude of 58 m. This site has a Scots pine monoculture and an understory composed primarily of cowberry (*V. vitis-idaea L.*) and lichens. The soil profile is a podzol and the humus form is a mor. The soil is nutrient-poor sediment soil and the soil texture is fine sand. The Scots pine monoculture was 119 years old in 1980. Annual mean temperature is 1.3°C and annual mean precipitation is 650 mm.

Site **Manjärv (No 3:1)**, north Sweden, about 70 km west of the city Luleå located at 65°47'N; 20°37'E at an altitude of 135 m. The stand has a Scots pine monocultures (46 years old in 1980) located on sediment soil. The stand has an understory composed mainly of cowberry and lichens. The humus form is mor and the soil profile a podzol. The soil texture is fine sand. Annual mean temperature is 1.0°C and annual mean precipitation is 700 mm.

Site **Norrliden (No 4)**, in north-west Sweden about 100 km north-west of Umeå is located at 64°21'N; 19°46'E at an altitude of 260 m. The site has a Scots pine monoculture (33 years old in 1986) with an understory composed mainly of bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*), located on till. Annual mean temperature is 1.3°C and annual mean precipitation is 595 mm.

Site **Granö (No 26)**, in north Sweden about 100 km northwest of the city of Umeå is located at 64°19' N; 19°02'E at an altitude of 300 m. The site has a Scots pine monoculture (41 years old in 1990) with an understory composed mainly of bilberry.

Site **Jädraås (No 6:51)** in Central Sweden, about 200 km north of Stockholm has a Scots pine monoculture. The plot (No 6:51) is sometimes also called Ih 5. It has a forest about 130 years old (in 1980) located at 60°49'N; 16°30'E at an altitude of 185 m. The forest is situated on a very nutrient-poor sediment soil. The annual mean precipitation is 609 mm and the long-term average temperature is 3.8°C. The understory is composed mainly of bilberry, cowberry, heather, mosses and lichens. The humus form is mor and the soil profile a podzol. The soil texture is fine sand. Additional information on this site provided by B. Axelsson and S. Bråkenhielm (1980).

Site **Brattforsheden (No 7)** in central west Sweden, is located at 59°38'N; 145°8'E at an altitude of 178 m. The site has a mature Scots pine monoculture on a sandy sediment soil with a low understory composed mainly of bilberry,

heather and cowberry. Annual mean temperature is 5.2°C and mean annual precipitation 850 mm.

Site **Nennesmo (No 8)**, in south-west Sweden, is located at 57°12'N; 13°35'E at an altitude of 155 m. The site has a mature Scots pine monoculture with a low understory composed mainly of bilberry, heather and cowberry. Annual mean temperature is 6.2°C and annual mean precipitation is 930 mm.

Site **Målilla (No 9)**, in south-east Sweden is located at 57°25'N; 15°40'E at an altitude of 105 m. The site has a mature Scots pine monoculture with a low understory composed mainly of bilberry, heather and cowberry. Annual mean temperature is 6.2°C and annual mean precipitation is 670 mm.

Site **Mästocka (No 10:1)** is located in south-west Sweden (56°36'N; 13°15'E and 135 m) has a Scots pine monoculture with a low understory of mainly bilberry. The soil texture is sandy till and the humus type is a more. Annual mean temperature was 6.8°C and annual mean precipitation is 1070 mm.

Site **Vomb (No 12)** is located in south Sweden (55°39'N; 13°19'E and 46 m) has a Scots pine monoculture with a low understory of mainly low grasses. The soil is sand and the humus type is a mor. Annual mean temperature is 7.0°C and annual mean precipitation is 770 mm.

Site **Roggebotzand (No 300)** at 52°34'N; 05°47'E and at an altitude of 5 m below s.l. is located on Flevoland in northern Netherlands. Annual temperature was 10.3°C and annual mean precipitation was 826 mm (average for 1988 and 1989). The site has a monoculture of Austrian pine (*Pinus nigra*) with a closed canopy and no understory. The organic layer is a podzol.

Site **Ehrhorn (No 13)** about 50 km south of Hamburg is located at 53°00'N; 09°57'E at an altitude of 81 m. The site has a mature Scots pine monoculture with an understory composed mainly of bilberry, heather and low grasses. Annual mean temperature was 8.7°C and annual mean precipitation was 644 mm.

Site **Czerlonka (No 23)** in east Poland is located at 52°41'N; 23°47'E at an altitude of 165 m. The site has a Scots pine monoculture with an understory composed mainly of bilberry and grasses. and the humus type is a mor. Annual mean temperature was 6.7°C and annual mean precipitation was 594 mm.

Site **Mierzwice (No 24)** in east Poland is located at 52°20'N; 22°59'E at an altitude of 142 m. The site has a mature Scots pine monoculture with a very sparse understory composed mainly of some grasses and some bilberry. Annual mean temperature was 7.2°C and annual mean precipitation was 569 mm.

Site **Pińczów (No 25)** in south Poland about 100 km north of Cracow is located at 50°31'N; 20°38'E at an altitude of 191 m. The site has a mature Scots pine monoculture with an uneven and sparse understory composed mainly of low grasses and some low herbs. The stand is located on nutrient poor sediment soil of granite origin. Annual mean temperature was 7.6°C and annual mean precipitation was 689 mm.

Site **Ede (No 14)** in central Netherlands is located at 52°02'N; 05°42'E at an altitude of 45 m. The site has a mature forest of Scots pine mixed with some oak

with an understory composed mainly of low grasses and low herbs. Annual mean temperature was 9.3°C and annual mean precipitation was 765 mm.

Site **La Gileppe (No 302)** in the Ardennes in east Belgium is located at 50°34'N; 05°59'E at an altitude of 370 m. The site has a mature Scots pine monoculture with an understory composed mainly of grasses. Annual mean temperature was 6.9°C and annual mean precipitation was 1200 mm.

Site **Wilków (No 22)** just north of Warsaw is located at 52°24'N; 20°33'E at an altitude of 74 m. The site has a mature Scots pine monoculture with a sparse understory composed mainly of bilberry. Annual mean temperature was 7.8°C and annual mean precipitation was 500 mm.

Site **Ołobok (No 28)** in west Poland just south of the town Świebodzin is located at 52°22'N; 14°36'E at an altitude of 60 m. The site has a mature Scots pine monoculture with an understory composed mainly of bilberry and low grass. Annual mean temperature was 8.1°C and annual mean precipitation was 604 mm.

Site **Bois de la Commenderie (No 303)** is located in north-central France south-east of Paris at 48°17'N; 02°41'E at an altitude of 83 m. The site has a mature Scots pine monoculture (30 years old in 1984). Annual mean temperature was 11°C and annual mean precipitation was 607 mm.

Site **La Viale (No 304)** is located in south France (Massif Central) at 44°11'N; 03°24'E at an altitude of 920 m. The site has a Scots pine monoculture (20-25 years old in 1991) with an understory composed mainly of low sparse grass. Annual mean temperature was 8.2°C and annual mean precipitation was 793 mm.

Site **Capelada (No 305)** is located in north-west Spain (Galicia) at 43°40'N; 07°58'W at an altitude of 447 m. The site has a mature Radiata pine (*Pinus radiata*) monoculture with an understory composed mainly of grass. Annual mean temperature was 12.9°C and annual mean precipitation was 1062 mm.

Site **Aguas Santas (No 306)** is located in north-west Spain (Galicia) at 42°44'N; 08°45'W at an altitude of 530 m. The site has a Maritime pine (*Pinus pinaster*) monoculture with an understory composed mainly of grass. Annual mean temperature was 12.5°C and annual mean precipitation was 1500 mm.

Site **El Raso (No 307)** is located in west Spain about 120 km north of Salamanca at 41°47'N; 05°26'W at an altitude of 760 m. The site has two plots, one with a Maritime pine monoculture (No 307:1) the other with a Stone pine monoculture (No 307:2) (both of them about 30-40 years old in 1990) with a very sparse understory composed mainly of grasses such as *Agrostis castellana*. Other species are *Tolpis barbata*, *Thymus mastichina*, *Echium vulgare*, and *Lupinus angustifolium*. The soils are chromic luvisols. Annual mean temperature was 12.1°C and annual mean precipitation was 402 mm.

Site **Furadouro (No 308)** in west central Portugal is located at 43°58'N; 09°15'W and at an altitude of 80 m.a.s.l. The site has a Maritime pine monoculture (No 308:1) and a mixed pine stand with Radiata pine and Maritime pine in proportions of about 1:1 (No 308:2). The plot has a scattered understory of low bushes of *Ulex spp*. Annual mean temperature was 15.2°C and annual mean precipitation was 607 mm.

The site **Albarese (No 309)** is located on the westcoast of central Italy, in Maremma Nature Reserve in Tuscany at 42°40'N; 11°10'E at an altitude of 11 m. The site has a mature Stone pine (*Pinus pinea*) monoculture with an understory composed mainly of grasses and herbs. Annual mean temperature was 15.0°C and annual mean precipitation was 650 mm.

The **Terzigno site** (No 310) (40°49'N; 142°9'E), located on the southeastern slope of Mount Vesuve, and 20 km southeast of Naples (Campania) has a forest of Stone pine, aged about 40 years (in 1990) planted on volcanic lapillus. The forest has a very sparse understory. At the latest eruption in 1944 the actual area was covered with a lapillus layer about 1 m thick which covers the soil of a former mixed forest. The altitude is 250 m.a.s.l., the annual mean temperature is 13.2°C and the annual mean precipitation 960 mm. The climatic data refer to the nearest meteorological station "Osservatorio Vesuviano" at an altitude of 612 m.a.s.l. (1926-1950).

The site **Golia Forest (No 311)** with a 50-80-year-old Corsican pine (*Pinus nigra var. laricio*) forest is almost completely dominated by this tree species. It is located in the Sila mountains (Calabria) at an altitude of 1210 m at 39°20'N; 16°27'E. The annual mean temperature is 9.0°C and the annual mean precipitation is 1225 mm. The climate data refer to the meteorological station of Cecita at the same altitude but 3 km distant from the Golia forest (1921-1950). The plot is situated on a weak slope to the south and the forest has an understory of adderspit (*Pteridium aquilinum*), and herbs in a lower frequency. It has a shallow, sandy soil on granite as parent material. The humus type is moder.

Site **Doñana (No 29)** in south-west Spain at 38°07'N; 06°12'W and an altitude of 2 m is located close to the coastline in the Doñana National Park. Annual mean temperature was 16.6°C and annual mean precipitation was 557 mm. The site has a mature Stone pine mono-culture and the ground is without understory.

The site **Mohican (No 401)** is located in north-east Ohio, USA at 40°36'N; 82°17'W and an altitude of 390 m a.s.l. The site has a Red pine (*Pinus resinosa Ait.*) monoculture about 43 years old (in 1991). The number of stems ha^{-1} was 869 and the trees' basal area was 41 m^2 ha^{-1} (in 1991). The soil was a Lordstown series sandy glacial till. Average annual temperature was 10.3°C and annual average precipitation 970 mm.

The site **Blue Rock (No 402)** is located in north-east Ohio, USA at 39°36'N; 81°51'W, and an altitude of 275 m a.s.l. The site has a Red pine monoculture about 40 years old (in 1991). The number of stems ha^{-1} was 891 and the trees basal area was 42 m^2 ha^{-1} (in 1991). The soil was a Berks silt. Average annual temperature was 11.9C and annual average precipitation 990 mm.

The site **Balls (No 403)** is located in north-east Ohio, USA at 40°41'N; 81°18'W and an altitude of 300 m a.s.l. The site has a Red pine monoculture about 33 years old (in 1991). The soil was a Muskingum silt loam. Average annual temperature was 9.7°C and annual average precipitation 960 mm.

The site **Athens (No 16)** is located just outside the town Athens in northeast

Georgia, USA at 33°53'N; 83°22'W and at an altitude of 207 m. The site has a Loblolly pine (*Pinus taeda*) monoculture about 19 years old (in 1986) and an understory of Sweet gum (*Liquidambar styraziflua*) and Flowering dogwood (*Cornus florida*). The soil was a cecil sandy clay loam. Average annual temperature was 16.5°C and annual mean precipitation 1049 mm.

The site **Tifton (No 16:2)** is located just outside the town of Tifton in south Georgia, USA at 31°28'N; 83°32'W at an altitude of 101 m. The site has a Loblolly pine monoculture about 30 years old (in 1986) and an understory of some Southern Magnolia (*Magnolia grandiflora*). The soil was an Alapaha loamy sand with 90 percent sand. Average annual temperature was 19.3°C and annual mean precipitation 1540 mm.

APPENDIX II

Correlation matrix based on all variables selected for use in regional analysis portion of this study (37 sites and subsets). Coefficients within parentheses are not significant on the $p < 0.05$ level

	LOSS	PET	PRECIP	AET	DEF	SUR	JULT	RNG	AVGT	NITR	PHOS	WSOL
LOSS	*	.42	.56	.70	-.33	.33	(0.19)	(.08)	.44	(-.00)	(.14)	(.19)
PET	.42	*	.35	.78	.47	(.00)	.91	(.20)	.97	(.11)	(.01)	.32
PRECIP	.56	.35	*	.69	-.43	.91	(.26)	.44	.34	(.07)	(.13)	(.27)
AET	.70	.78	.69	*	(-.19)	.33	.70	(.12)	.72	(.10)	(.19)	(.21)
DEF	-.33	.47	-.43	(-.19)	*	-.46	.44	(.14)	.51	(.03)	(-.25)	(.20)
SUR	.33	(.00)	.91	.33	-.46	*	(-.06)	.50	.03	(.04)	(.05)	(.23)
JULT	(.19)	.91	(.26)	.70	.44	(-.06)	*	(.08)	.85	(.15)	(.06)	(.24)
RNG	(.08)	(.20)	.44	(.12)	(.14)	.50	(.08)	*	(.25)	(.29)	(-.04)	(.01)
AVGT	.44	.97	.34	.72	.51	(.03)	.85	(.25)	*	(.09)	(- .09)	.34
NITR	(-.00)	(.11)	(.07)	(.10)	(.03)	(.04)	(.15)	(.29)	(.09)	*	.53	-.36
PHOS	(.14)	(.01)	(.13)	(.19)	(-.25)	(.05)	(.06)	(.04)	(.09)	.53	*	(-.06)
WSOL	(.19)	.32	(.27)	(.21)	(.20)	(.23)	(.24)	(.01)	.34	-.36	(-.06)	*

SOIL ORGANIC MATTER IN SOME EUROPEAN CONIFEROUS FORESTS

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Abstract. The amounts of total soil organic matter accumulated in the upper soil layers (the L+F+H layers) were sampled in coniferous forests, mainly pine forests in western Europe. Exactly the same techniques were used in most cases. The amounts of ash-free soil organic matter varied between 947 and 3227 $g \cdot m^{-2}$ for pine forests with the average value of 1977 $g \cdot m^{-2}$. A Norway spruce forest had 5665 $g \cdot m^{-2}$, and a Silver fir forest the extreme amount of about 110 000 $g \cdot m^{-2}$.

Comparisons were made between amounts of soil organic matter and latitude for pine forests and a clearly significant relation was seen. When the ash-free amounts and total precipitation were compared for all sites a relation was seen with $p < 0.1$.

Key words: Soil organic matter, transect, pine forests coniferous forests, humus.

INTRODUCTION

Soil organic matter is in many soils the main carrier and the source of readily available nutrients and is also of importance for the soil's water balance. It further provides the soil organisms with an energy source for their activity, which is the basis for nutrient release.

The main inflow of organic matter to the soil is through litterfall and in forest systems that from the trees normally dominates. The chemical composition of these materials plus the temperature and moisture of soil are the main factors for the turnover rates of the organic layers and as regards both quantity and quality of nutrient release. These factors together plus the composition of the soil microbial population determine the rate of soil layer turnover and the magnitude of a net storage of organic material.

For a long time there was a relatively low interest in the quantities of soil organic matter and until the period of the International Biological Program in the 1970-ies comparatively few measured values were published. In that period when larger ecosystem projects involved several branches of science into combined efforts, several critical study areas were revealed. As a consequence several quantitative measurements of the amounts of soil organic matter were carried out as well as of amounts of falling litter.

The aim of this report has been to present some data about the current knowledge of the amounts of soil organic matter in forest systems. The present study gives

data on the upper organic soil layers from some differing European coniferous forest types.

SITE DESCRIPTIONS

The approximate locations for the sites are given on a map (Figure 1). The site numbers 2 to 109 given on the map and in the text and tables are the same as those used by B. Berg et al. (1986; 1991). Some site data are given in Table 1.

Table 1. Some data for the investigated sites

Site No/Name		Tree species	Lat./ Long.	Altitude (m a. s. l.)	Mean annual		Understory
					precip. (mm)	temp. (°C)	
2	Harads	Scots pine	66°08'N; 20°53'E	58	650	1.3	*V. vitis-idaea*, lichens
6:51	Jädraås	Scots pine	60°49'N; 16°30'E	185	609	3.8	*V. vitis-idaea*, *V. myrtillus*, lichens, mosses, *C.vulgaris*
109	Garpenberg	Norway spruce	60°16'N; 16°15'E	185	650	4	*V. myrtillus*, *C. vulgaris*
300	Roggebotzand	Austrian pine	52°34'N; 05°47'E	-5	826	10.3	None
307:1	El Raso	Stone pine	41°47'N; 05°26'W	760	400	11.4	Thin grass
307:2	El Raso	Maritime pine	41°47'N; 05°26'W	760	400	11.4	Thin grass
29	Doñana	Stone pine	38°07'N; 06°12'W	2	557	16.6	None
312	Monte Taburo	Silver fir	41°05'N; 12°27'E	1100	2166	7.9	Some herbs
308:1	Furadouro	Maritime pine	39°25'N; 09°15'W	80	607	15.2	None
308:2	Furadouro	Monterey pine	39°25'N; 09°15'W	80	607	15.2	None
313	Vallgorguina	Monterey pine	41°40'N; 02°30'E	260	736	13.6	Some young oaks
314	Santa Coloma	Monterey pine	41°52'N; 02°38'E	200	750	15.6	Some young oaks and chestnuts, some grass

Site **Harads (No 2)** is located at 66°08'N; 20°53'E at an altitude of 58 m. This site with an 129-year-old (in 1990) forest of Scots pine (*Pinus silvestris*) has an understory composed primarily of cowberry (*V. vitis-idaea* L.) and lichens. The annual mean temperature was 1.3°C and the annual mean precipitation 650 mm. The soil profile is a podzol and the humus form is a mor. The soil is

Fig 1. Map of Europe giving the approximate positions for the sites used (cf Table 1)

nutrient-poor sediment and the soil texture is fine sand. The Scots pine monoculture was 129 years old (in 1990).

Site **Garpenberg (No 109)** is located at 60°16'N; 16°15'E at an altitude of 185 m. The annual mean temperature and precipitation are 4°C and 650 mm resp. (measured at the station Risfallet, 20 km to the S.W. at the same altitude). The Norway spruce (*Picea abies*) monoculture has an understory of bilberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*). The humus form is moder, the soil profile a podzol and the soil texture clayey till. The forest stand was 123 years old in 1990.

Site **Jädraås (No 6:51)** in Central Sweden has a Scots pine monoculture about 140 years old (in 1990) and is located at 60°49'N; 16°30'E at an altitude of 185 m. The forest is situated on a very nutrient-poor sediment soil. The annual mean precipitation is 609 mm and the long-term average temperature is 3.8°C.

The understory is composed mainly of bilberry, cowberry, heather, mosses and lichens. The humus form is a mor and the soil profile a podzol. The soil texture is fine sand. Further site data are given by B. Axelsson and S. Bråkenhielm (1980).

Site **Roggebotzand (No 300)** at 52°34'N; 05°47'E and at an altitude of 5 m below s.l. is located on Flevoland in the northern Netherlands. The annual average precipitation is 826 mm and the annual mean temperature 10.3°C. The site has a monoculture of Austrian pine (*Pinus nigra*) 33 years old (in 1990) and no understory. Tree density was 1600 ha^{-1}. Canopy cover was 80 percent. The forest is located on recently reclaimed polderland. The organic layer is a mor. The litter layer was 2.8 cm thick and the humus layer which was 2.7 cm deep on the average (25 measurement points) had a pH of 6.4 (0-2 cm). Soil type is unknown and soil texture is sand. Formation of a podzolic soil has just started.

Site **El Raso (No 307)** is located the western part of Spain on a high plateau at 41°47'N; 05°26'W and at an altitude of 760 m a.s.l. Annual mean temperature is 12.1°C and annual mean precipitation 402 mm. The annual actual evapotranspiration is 391 mm and the annual potential evapotranspiration 700 mm. The site is divided into two plots each measuring 50 m × 50 m. One of the plots has a plantation of Maritime pine (*Pinus pinaster*) about 30-40 years old (in 1990) with a canopy cover of 59 percent (as measured by Cajanus tube, cf. Lindroth and Perttu, 1981). The other plot planted with Stone pine (*Pinus pinea*) had a stand of about the same age with a canopy cover of about 43 percent (Cajanus tube). The plots have both a sparse understory dominated by grass such as *Agrostis castellana*. Other species found are *Tolpis barbata*, *Thymus mastichina*, *Echium vulgare*, and *Lupinus angustifolium*. The litter layers were 0-0.5 cm and 0-0.2 cm on the average for the Maritime pine and the Stone pine stands respectively and humus layers were not formed.

Site **Furadouro (No 308)** in west central Portugal is located at 39°25'N; 09°15'W and at an altitude of 80 m a.s.l. The site corresponds to a field trial which was established to follow the above-ground biomass production of eucalypt and pine species and includes four plots (50 m × 50 m) planted with Maritime pine (*Pinus pinaster*) and four planted with Monterey pine (*Pinus radiata*). Both plantations were 23 years old in 1990 and without any understory (some low Ulex bushes were removed in 1989). The site is located on Cretacic sandstones covered by Pleiocenic sand. The soils are mostly Spodosols with a sandy texture. The clay content is lower than 5 percent down to 60 cm depth. The pH and the organic carbon content in the upper 15 cm layer varies, respectively in the range of 4.6 to 5.6 and of 0.56 and 2.02 percent. Annual mean temperature and precipitation are respectively 15.2°C and 607 mm, with the dry season from June to September having an average of less than 10 percent of the annual precipitation. The climate is Mediterranean, tempered by the oceanic influence. Climatic data refer to the nearest meteorological station "Caldas da Rainha" (1941-1970) located at an altitude of 70 m a.s.l. and 10 km from the site. The spacing of the plantation was 3 m.

Site **Doñana (No 29)** in southwestern Spain at 38°07'N; 06°12'W and at an altitude of 2 m a.s.l. is located close to the coastline in the Doñana National Park.

The annual average temperature is 16.6°C and the annual mean precipitation 557 mm. The annual actual evapotranspiration is 479 mm and annual potential evapotranspiration 871 mm. The site has a Stone pine monoculture and the ground is without any understory. The stand was about 44 years old (in 1990).

Site **Monte Taburno (No 312)** in southern Italy (41°05'N; 12°27'E) has an 80-to-100-year-old forest of Silver fir (*Abies alba*), planted on a site formerly covered by a forest of common beech (*Fagus sylvatica*) is located at an altitude of 1100 m a.s.l. about 42 km northeast of Naples (in the province of Campania). The forest has a dense canopy cover with about 91 percent coverage as measured by the Cajanus tube (Lindroth and Perttu, 1981). The annual mean temperature is 7.9°C and the annual mean precipitation is 2166 mm. The plot is situated on a weak slope to the west. The ground, which has a poor understory of herbs has a mull soil with an organic layer estimated to be more than 1 m thick. The upper organic layer has a pH of about 6, a C-to-N ratio of 12 and the organic matter content is 35.3 percent in the upper 0-5 cm and 25.2 in the 5-10 cm layer. The parent material is limestone and the deeper profile for this site has been described for a nearby beech forest by A. Virzo de Santo et al. (1976). The climatic data refer to the nearest meteorological station on Mount Montevergine (1921-1963) at 1270 m altitude and about 10 km from the site.

Site **Vallgorguina (plot No 313:RO)** is located about 54 km north of Barcelona in northeastern Spain at 41°40'N; 02°30'E at an altitude of 260 m a.s.l. The annual mean precipitation is 736 mm and annual mean temperature 13.6°C. The forest, 31 years old (in 1990) is a Monterey pine monoculture with a sparse and low understory of oak (*Quercus ilex*) and *Arbutus unedo*. The former use of this plot was a vineyard. The parent rock is granodiorite.

Site **Santa Coloma de Farners (plot No 314:MA)** is located about 100 km north of Barcelona in northeastern Spain at 41°52'N; 02°38'E at an altitude of 200 m a.s.l. The annual mean precipitation is 750 mm and annual mean temperature 15.6°C. The forest, 19 years old (in 1990) is a Monterey pine monoculture with a sparse and low understory of oak (*Quercus ilex*), chestnut (*Castanea sativa*), *Pteridium aquilinum* and *Hedera helix*. The former use of this plot was for cultivation of chestnut. The parent rock is granite.

MATERIALS AND METHODS

SAMPLING METHOD AND EXPERIMENTAL DESIGN

The basic soil sampling units were the litter (L) layer and humus (F plus H) layers, which make up the forest floor. All live plant material such as mosses, lichens, shrubs and root material were not considered as part of the forest floor. The fine root material, however, was not removed from the sampled F and H layers for practical reasons.

The sampled plots had the following dimensions; site Harads 10m × 30 m, site Garpenberg 40 m× 40 m, site Jädraås 100 m × 200 m, sites Roggebotzand, El

Raso, Doñana, and Monte Taburno, 50 m × 50 m. The sites Vallegor-guina and Santa Coloma measured 20 m × 20 m. At site Terzigno an irregular area of about 2500 m^2 was sampled. At the Furadouro site the samples were collected in a block design, namely three plots each measuring 30 m × 30 m.

The litter and humus layers were sampled using square soil corers which for the sites Harads, Garpenberg and Jädraås measured 14.2 cm × 14.2 cm giving a surface of 201.4 cm^2. For the sites Roggebotzand, El Raso, Doñana the sampler measured 20 cm × 20 cm giving a surface area of 400 cm^2, at the site Furadouro 50 cm × 50 cm giving a surface of 2500 cm^2. At the sites Vallgorguina and Santa Coloma a circular sampler was used with a diameter of 21 cm thus giving a surface of 346.2 cm^2. At site Furadouro 15 samples were taken in a block design; at the other sites the number of replicates was 20-25. The site Monte Taburno which had an extremely thick organic layer had 4 replicate samples, taken with a soil corer measuring 10 cm × 4 cm. Two replicate samples were analyzed for bulk density (see below).

TREATMENT OF SAMPLES

Both the litter layer and the humus layer were normally collected together. At the sites Jädraås, Furadouro, Santa Coloma and Vallgorguina these two layers were, however, collected separately. The material was sorted by hand and all living biomass removed. All material was dried at 85°C or 105°C and weighed, after which ash was determined.

At the sites Monte Taburno and Terzigno samples were analysed by loss-on-ignition and bulk density was measured to be 0.68 $g \cdot cm^{-3}$ for the upper 0-11 cm and assumed to be the same in the whole profile.

CARBON ANALYSIS

At the sites Vallgorguina and Santa Coloma no ash determination was made but the soil samples were analysed for carbon.

ASH DETERMINATION

Each single sample was ground individually in a laboratory mill equipped with a screen allowing particles of less than 1 mm to pass. Ash was determined by heating subsamples at 600°C for 2 h.

TERMINOLOGY

For the purpose of this paper we have adopted the terminology "soil organic matter" (S.O.M.) to mean the total sampled dead organic material in the forest floor unless there is a clearly stated subdivision into litter and humus.

For the pine species *Pinus radiata* we have used the the correct English name *viz*. Monterey pine, although a commonly used name is also Radiata pine.

RESULTS AND DISCUSSION

GENERAL COMMENTS

The sites had forests of very different ages and the site history was often little known, facts that may prevent some comparisons and conclusions about the material. The comments below are therefore mainly restricted to presentation of data. All values given are on an ash-free basis.

INDIVIDUAL SITES

Site **Harads (No 2)**. In spite of its age (129 years) this Scots pine stand had a relatively thin layer of soil organic matter, about 1.4 cm with a mass of 2529.3 $g \cdot m^{-2}$ above the mineral soil (Table 2). As this site was subject to a fire about 140 years ago the present amount of soil organic matter has accumulated from litter of the present stand.

Site **Jädraås (No 6:51)**. This site, with a Scots pine forest that was about 120

Table 2. Amounts of ash-free soil organic matter in the organic soil layer (forest floor) in some coniferous forest systems. Standard deviations are given within parenthesis

Site name	Tree species	Stand age[2] (years)	Amount ($g \cdot m^{-2}$)	S. D.	C. L. (95%)	n
Pine						
Harads	Scots pine	ca 129	2529.3	1601.9		25
Jädraås	Scots pine	130	2262		< 740	24
Roggebotzand	Austrian pine	33	2595.6	1111.5		25
El Raso	Stone pine	30-40	1496.1[1]	1107.4[1]		25
El Raso	Maritime pine	30-40	1749.3	938.8		24
Doñana	Stone pine	45	1155.0	679.4		25
Furadouro	Maritime pine	23	2831	924		15
Furadouro	Monterey pine	23	3232	806		15
Vallgorguina	Monterey pine	32	2010.2	1250		20
Santa Coloma de Farners	Monterey pine	20	1633	440		20
Spruce						
Garpenberg	Norway spruce	123	5664.7	1463.3		25
Fir						
Monte Taburno	Silver fir	80-100	108 800			

[1] With an extreme value excluded, the amount became 1304 m^{-2} and SD 595.8
[2] In 1990

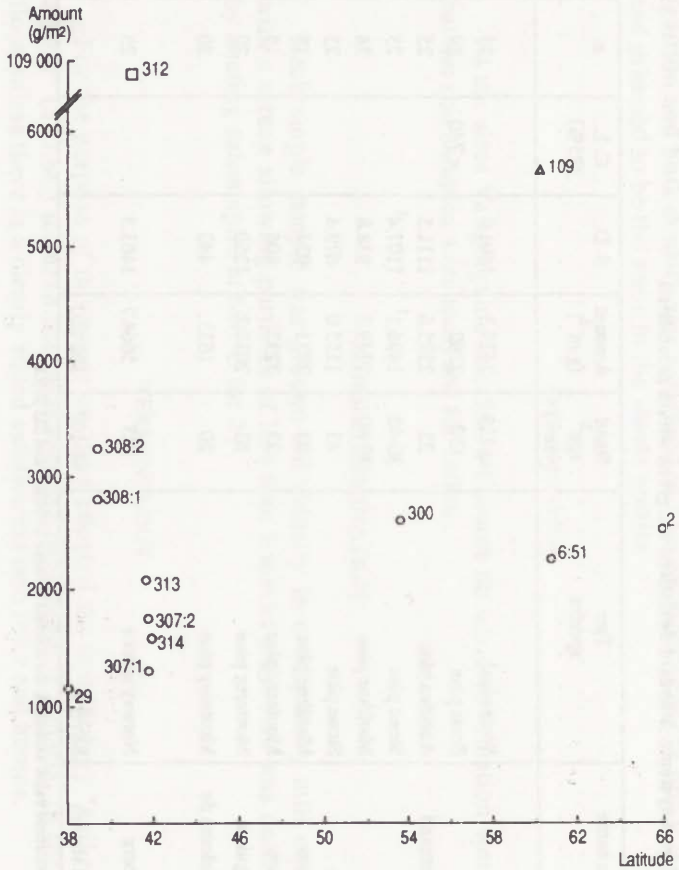

Fig 2.A. The amount of soil organic matter compared to the site's latitude (o) pine forests, (Δ) Norway spruce site, (❑) Silver fir site

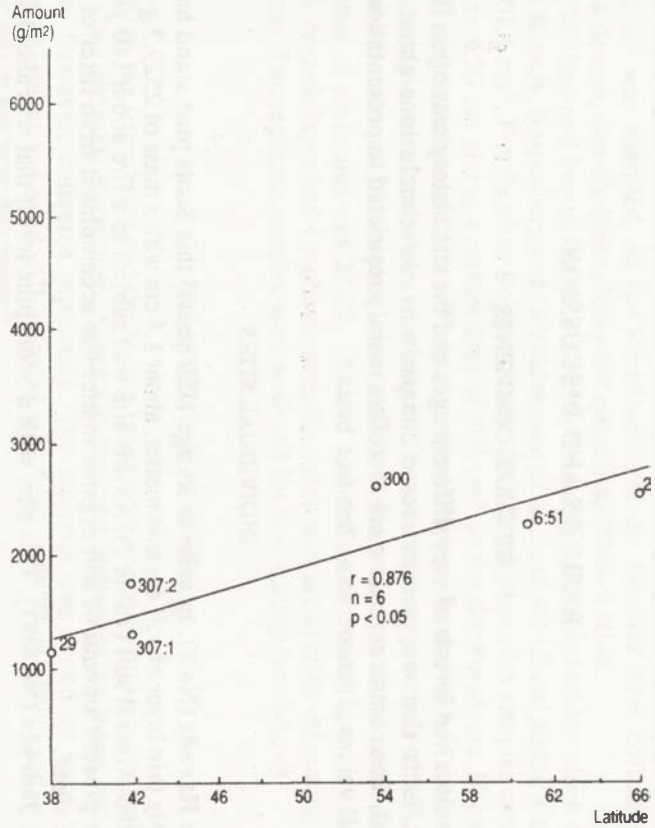

Fig. 2B. Linear regression between latitude and amount of soil organic matter for pine sites at which a unified sampling technique was applied

years old at sampling of the soil organic matter, was completely burnt around 1850 and the remaining coal was to be found in the lowest part of the soil profile. We might therefore consider this layer as being built up exclusively by the present stand. The total amount was 2262 $g \cdot m^{-2}$ with 95 percent confidence limits of 740. A smaller part came from the litter layer (715 $g \cdot m^{-2}$) and a higher amount from the humus layer (1540 $g \cdot m^{-2}$) of which layers the latter was on the average 4.5 cm thick and relatively even (Table 2). Data presented earlier by H. Staaf and B. Berg (1977).

Site **Roggebotzand (No 300)**. This site with a monoculture of Austrian pine had a soil organic matter layer about 5.5 cm deep and the total amount of dead organic matter accumulated in the forest floor was 2595.6 $g \cdot m^{-2}$ (Table 2). This stand was planted on the mineral soil of a reclaimed land and also in this case the amount of soil organic matter originates from litter of the present stand.

Site **El Raso (No 307)**. At site El Raso two plots were sampled, one with Stone pine and one with Maritime pine. The soil organic matter of the forest floor was very sparse and no real humus layer could be seen in either case. The two sites had amounts of organic matter that were similar in magnitude with 1496 and 1749 $g \cdot m^{-2}$ (Table 2). There was no significant difference between them.

Site **Furadouro (No 308)**. At site Furadouro six plots were sampled in a block experiment, with three plots of each of Maritime pine and Monterey pine. The soil organic matter layer had an overall thickness of 2 to 5 cm. Both litter and humus layers were present and easily distinguished. The latter had a dense mycelium framework and significant amounts of pine fine roots. The litter layers consisted exclusively of finer litter components.

The forest floor in the stand of Maritime pine had an amount of soil organic matter of 2831.3 $g \cdot m^{-2}$ (Table 2). This amount came partly from the litter layer (1031 $g \cdot m^{-2}$) and the humus layer (1800.3 $g \cdot m^{-2}$). The amount of soil organic matter in the forest floor of the Monterey pine stand was 3232.3 $g \cdot m^{-2}$. This amount came from the litter layer (549.9 $g \cdot m^{-2}$) and partly from the humus layer (2682.4 $g \cdot m^{-2}$). There was no significant difference between the two stands as regards the total amounts of soil organic matter. There was, in contrast, a significant difference when the amounts of the litter layers were compared. For the Maritime pine the litter layer was no less than 36.4 percent of the total soil organic matter, while in the Radiata pine stand it was 17 percent.

Site **Doñana (No 29)**. This site had a Stone pine monoculture and a litter layer consisting exclusively of pine litter. No humus layer had been formed. The amount of organic material was 1155 $g \cdot m^{-2}$ (Table 2). It appears from the standard deviation that this site had the most evenly distributed organic layer of the sites investigated.

Site **Vallgorguina (No 313)**. This site with Monterey pine on an old vineyard soil had an amount of soil organic matter of 1166 $g \cdot m^{-2}$ (Table 2).

Site **Santa Coloma (No 314)**. This site with a Monterey pine monoculture on the land of a former chestnut plantation had a total amount of soil organic matter of 947 $g \cdot m^{-2}$ (Table 2).

Site **Garpenberg (No 109)**. This site with Norway spruce had an amount of soil organic matter of 5665 $g \cdot m^{-2}$ (Table 2).

Site **Monte Taburno (No 312)**. The site Monte Taburno was in terms of soil organic matter an extreme site with a soil organic matter layer of more than 100 cm depth and the sampling design had to be adapted to this and was thus different from that of the other sites. A direct comparison therefore may seem not to be entirely correct. However, the value of about 110 000 $g \cdot m^{-2}$ (down to 1 m depth) was very high (Table 2; Figs 2a, 3a). We may, therefore, with respect to the fact that the value was extreme, make some comparisons. As the soil was a mull the ash content was relatively high. The layer investigated could in part have been formed by earlier stands of beech.

COMPARISON OF SITES

Some attempts to compare the amounts of S.O.M. to available environmental parameters were made although there are severe limitations to such comparisons. The different ages of the stands and the often lacking site history as well as the varying sampling design restricts the possibilities to analyse the data. However, on a crude scale some intersite comparisons may be made. Assuming that the genus Pinus may have some properties in common across the species we compared the amounts in pine forests to the annual mean precipitation, and to the latitude. These two comparisons did not give any significant relation.

In another comparison the pine sites were compared at which an identical sampling technique was used, *viz.* the sites Nos 2, 6:51, 300, 307:1, 307:2 and 29. When compared to latitude a significant positive linear relation was seen ($r=0.876$; $n=6$; $p < 0.05$) suggesting more soil organic matter further to the north within this region. In a comparison to precipitation a positive linear relation ($r=0.751$; $n=6$; $p < 0.1$) was seen. Although this relation is not really significant it still hints that sites with a higher precipitation should have higher amounts of soil organic matter. In support of this it may be added that this extreme site (No 312) with a Silver fir forest also had an extremely high amount of soil organic matter (cf Table 2; Fig 3).

CONCLUDING REMARKS

The number of sites investigated in the present study is really too small to allow any good conclusions to be drawn. One comment that is justified is that the driest sites appear to have low values, irrespective of stand age. The site with an estimated extreme amount of soil organic matter — Monte Taburno, appeared also to have a very high precipitation. Such a connection may be reasonable. A high precipitation may support a higher biomass and litter production and may further slow down litter and humus decomposition. A high precipitation may also prevent forest fires from burning up the the organic material, a phenomenon known to have happened fre-

quently in e.g. northern Scandinavia. We may speculate upon whether the observed high amount for the Monte Taburno site would be common in those parts of Europe that have a high precipitation e.g. the west coast of Spain, Scotland, or the Appenines. Also the amount found at site Garpenberg was higher than the average value for pine.

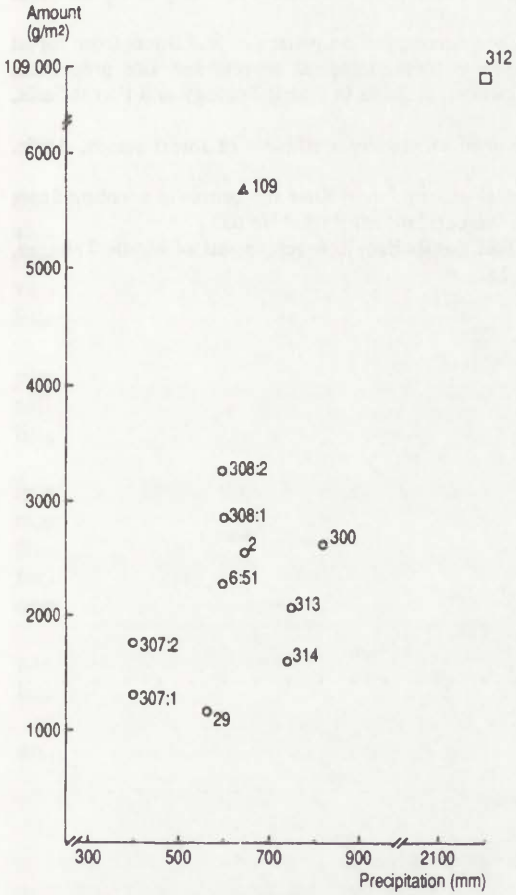

Fig 3A. The amount of soil organic matter compared to the site's annual precipitation: (o) pine sites, (Δ) Norway spruce site, (□)) Silver fir site

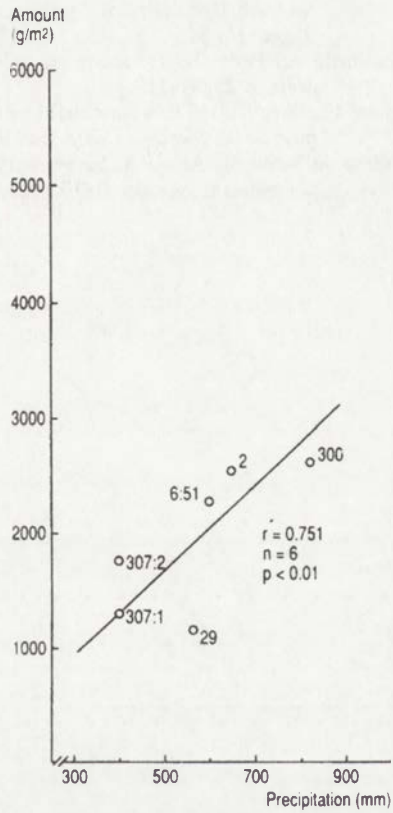

Fig. 3B. Linear regression between the amount of soil organic matter and precipitation for pine sites at which a unified sampling technique was applied

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AMOUNTS OF LITTERFALL IN SOME EUROPEAN CONIFEROUS FORESTS

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Abstract. Litterfall data, mainly needle litter were available for 33 sites in Scandinavia and for a further six sites in Western Europe mainly for needle litter were available. Regressions were calculated for total litterfall and needle litterfall. The best simple regression relationships were obtained with latitude, site index and basal area as predictor variables, whereas the regression on stand age was significant only for the fraction "other litter".

Multiple regression relationships including that between needle litterfall and latitude plus basal area and that including site index plus basal area plus latitude, were highly significant. For total litterfall, the r^2 values were 0.71 and 0.77 respectively and for needle litter, the r^2 values were 0.81 and 0.82 respectively.

When all available data for Scandinavia were used, latitude and site index were highly significant (n=33 with r^2 values of 0.428 and 0.426 respectively). In multiple linear regressions all of the combined factors gave highly significant relation with r^2 values from 0.491 for site index plus basal area and 0.539 for latitude plus basal area. A three-factor model, using the above variables gave an r^2 value of 0.528, but this still explains only a little more than half of the variation.

When using all European data we obtained a highly significant linear relationship for needle litterfall and latitude and for a multiple linear relationship using age, altitude and latitude was highly significant with an r^2 value of 0.55 (n=38).

Key words: litterfall, pine, Scandinavia, Europe, stand age, site index, latitude, basal area.

INTRODUCTION

Litterfall, in north European forest systems dominated by litter from the trees, is the largest source for the inflow of organic material and nutrients to the forest floor. The chemical composition of this material, and the temperature and moisture content of the upper soil layers, are the main factors which control the turnover rates of the organic layers, as well as determining both the quantity and quality of nutrient release.

These factors, together with the composition of the soil microbial population, determine both the rate of turnover of soil layers, and whether or not net storage of organic material will occur. Today, it is possible to predict for a single ecosystem how a certain litter will change chemically during the course of decomposi-

tion. Given information on the initial chemical composition, and on chemical changes during decomposition, it is possible to predict how the mass-loss rate will change during the decomposition process.

For a long period, there was comparatively little interest in the chemical composition of litterfall, and until the time of the International Biological Programme (IBP) in the 1970s, rather few measured values were published. When major ecosystem projects integrated different scientific disciplines into a combined effort, several weak points were revealed in our knowledge of ecosystems: among these were the amount of litterfall and its chemical composition.

The aim of this paper is to identify and present the state of knowledge concerning the amounts of litterfall in European pine forest systems. The study has focussed on North-European forest types but Mediterranean sites are also included.

SITE DESCRIPTIONS

Additional data are given in Table 1.

The site **Skällarimsheden (No. 100)**, the northernmost in this series (66°32'N; 20°11'E), is situated immediately south of the Arctic circle at an altitude of 280 m above sea level (a.s.l.). The annual mean temperature is -0.5°C, the annual mean precipitation 500 mm. The site carries a Scots pine (*Pinus silvestris* L.) monoculture, about 98 years old (in 1980), growing on a nutrient-poor sediment. The soil is a podzol with mor as the humus form; the soil texture is sandy till. The field and bottom layer consist of cowberry (*Vaccinium vitis-idaea* L.) and lichens.

The site **Harads (No. 2)** is situated at 66°08'N; 20°53'E, 58 m a.s.l. This site carries a Scots pine monoculture, with a field and bottom layer composed primarily of cowberry and lichens. The soil type is a podzol and the humus form is mor. The soil has developed on a nutrient-poor sediment, fine sand in texture. The Scots pine monoculture was 119 years old in 1980. The annual mean temperature is 1.3 °C and the annual mean precipitation, 650 mm.

The site **Manjärv (No. 3)**, situated at 65°47'N; 20°37'E, 135 m a.s.l., has been subdivided into three plots (cf. Table 1) of differing nutrient status. All plots carry Scots pine monocultures, growing on sediment of varying richness and particle size distribution (Berg et al. 1991a). The most nutrient-poor plot (No. 3:1) has a Scots pine monoculture, about 46 years old (in 1980), with a field and bottom layer consisting mainly of cowberry and lichens. The humus form is mor and the soil type is a podzol. The soil texture is fine sand. Plot No. 3:2, intermediate in soil fertility, has a field layer consisting mainly of bilberry (*Vaccinium myrtillus* L.). The Scots pine monoculture was 49 years old (in 1980). The soil texture is silty, the soil type a podzol and the humus form a mor. The most nutrient-rich plot (No. 3:3) also carries a Scots pine monoculture, 48 years old (in 1980), with grass and herbs forming the field layer. The soil texture is silty, the humus form a mor and the soil type a podzol. The annual mean temperature is 1.0 °C and the annual mean precipitation, 700 mm.

Table 1. Some data for the sites used

Site No.	Name	Humus form	Soil texture	Stand agc[3] (y)	Basal area (m^2ha^{-1})	Site index (-)
100	Skällarimsheden	mor	sandy till	97	17.5	17
2	Harads	mor	fine sand	118	9.7	12
3:1	Manjärv	mor	fine sand	45	16.1	24
3:2	Manjärv	mor	silt	48	22.3	25
3:3	Manjärv	mor	silt	47	18.6	26
101	Västbyn[1]	mor	clayey till	70	36.0	24
6:51	Jädraås	mor	fine sand	125	15.0	16
6:Ih 4	"	mor	fine sand	60	20.0	17
6:Ih 3	"	mor	fine sand	22	5.0	21
102	Tomta	mor-moder	glacial clay	50	32.8	27
103	Kungs-Husby	mull	glacial clay	69	31.0	23
104	Dimbo	moder	fine sand-medium sand	53	27.8	29
105	Grensholm	mull	glacial clay	58	28.1	29
106	Remningstorp	mull-like moder	glacifluvial gravelly sand	60	23.0	27
107	Tveten	mor	sandy till	58	23.8	28
108	Sänksjön	mor	fine sand-medium sand	68	18.3	16
10:1	Mästocka[2]	mor	sandy till	57	20.0	26
300	Roggebotzand			33		
308:1	Furadouro			24		
308:2	Furadouro			24		
29	Doñana			45		
313	Vallgorguina			18	20.9	
314	Santa Coloma de Famers			20	31.0	

1. Site sometimes denominated Frösön (cf Johansson 1986); 2. Site sometimes denominated Kullavägen (cf Johansson 1986); 3. In 1979

The site **Västbyn (No. 101)**, with a Scots pine monoculture, 71 years old in 1980, is situated at 63°. 13'N; 14°28'E, 325 m a.s.l. The annual mean temperature is 2.0 °C and the annual mean precipitation, 455 mm. The field layer consists of bilberry, and the soil is a Dystric Cambisol. The humus form is mor. The texture is clayey till.

The site **Jädraås (No. 6)**, in Central Sweden, carries a Scots pine monoculture. The site has three plots: No. 6:51 (also called Ih 5) has a stand about 130 years old (in 1980), a younger stand ca 62 years old (in 1980; also called Ih 4) and a stand ca 25 years old (in 1980; also called Ih 3). The site is situated at 60°49'N; 16°30'E, 185 m a.s.l. The stands are growing on a very nutrient-poor glacifluvial sediment. The annual mean precipitation is 609 mm and the long-

term annual mean temperature is 3.8°C. The field and bottom layer consist mainly of bilberry, cowberry, heather (*Calluna vulgaris* (L.) Hull.), mosses and lichens. The humus form is mor and the soil type a podzol. The soil texture is fine sand. Further site data are given by Axelsson and Bråkenhielm (1980).

The site **Tomta (No. 102)**, situated in Central Sweden (59°49'N; 16°33'E) on a Eutric Cambisol with a mor-moder as humus form, carries a monoculture of Scots pine, 54 years old in 1980. The site lies at an altitude of 63 m a.s.l. and has a field layer of grass and bilberry. The annual mean temperature is 5.0 °C and the annual mean precipitation, 500 mm.

The site **Kungs-Husby (No. 103)** is situated in Central Sweden (59°31'N; 17°16'E), 30 m a.s.l., on a Eutric Cambisol with mull as humus form, and carries a 70-year-old (in 1980) monoculture of Scots pine. The soil texture is glacial clay and the field layer is composed of grasses and bilberry. The annual mean temperature is 5.3°C, the annual mean precipitation, 470 mm.

The site **Dimbo (No. 104)**, at 59°07'N; 15°44'E, 70 m a.s.l., is situated on a podzol soil with moder as humus type. The site carries a Scots pine monoculture (54 years old in 1980) with a field layer of grass. The soil texture is fine sand to medium sand. The annual mean temperature is 5.5°C and the annual mean precipitation, 550 mm.

The site **Grensholm (No. 105)**, situated in southern Sweden at 58°33'N; 15°51'E, 58 m a.s.l., has a 59-year-old monoculture of Scots pine growing on a Eutric Cambisol with mull as the humus form. The soil texture is glacial clay and the field layer consists of tall herbs and grass. Annual mean temperature is 6.1°C and the annual mean precipitation, 525 mm.

The site **Remningstorp (No. 106)**, situated in southern Sweden at 58°24'N; 13°39'E, 128 m a.s.l., carries a Scots pine monoculture (61 years old in 1980) with a field layer of low herbs and dwarf shrubs. The soil texture is glacifluvial gravelly sand, the humus form moder to mull-like moder and the soil type is a podzol. The annual mean temperature is 5.4°C and the annual mean precipitation, 550 mm.

The site **Tveten (No. 107)** in south Sweden (58°06'N; 13°17'E; 170 m a.s.l.) carries a monoculture of Scots pine, with a field layer of bilberry. The soil texture is sandy till, the humus form a mor and the soil type a podzol. The forest stand was 60 years old in 1980. The annual mean temperature is 5.4°C and the annual mean precipitation, 600 mm.

The site **Sänksjön (No. 108)**, situated at 58°04'N; 14°08'E, 245 m a.s.l., carries a Scots pine monoculture (69 years old in 1980), with a bottom layer mainly consisting of lichens. The soil texture is fine sand to medium sand, the humus form a mor and the soil type a podzol. The annual mean temperature is 5.1°C and the annual mean precipitation, 595 mm.

The site **Mästocka (No.10:1)**, situated at 56°36'N; 13°15'E, 135 m a.s.l., carries a Scots pine monoculture (54 years old in 1980), with a field layer mainly of bilberry. The soil texture is sandy till and the humus type is a mor. The annual mean temperature was 6.8°C and the annual mean precipitation, 1070 mm.

The site **Roggebotzand (No.300)**, at 52°34'N; 05°47'E, altitude 5 m below

sea level, is situated on Flevoland in the northern Netherlands. The annual mean temperature is 10.3°C and the annual mean precipitation, 826 mm (average for the years 1988 and 1989). The site carries a monoculture of Austrian pine (*Pinus nigra* Arnold var. *nigra*), 33 years old (in 1990) with no field or bottom layer. Tree density was 1600 ha^{-1}. The canopy cover, as determined by Cajanus tube (Lindroth and Perttu, 1981) was 81 per cent in 1988. The forest is situated on recently reclaimed polderland. The formation of a podzolic organic layer has just started. The litter layer had a thickness of 2.8 cm and the humus layer 2.7 cm on the average (as measured in 25 places within the plot) and a pH of 6.4 (0-2 cm depth). Soil type is unknown and soil texture is sand.

Site **Furadouro (No 308)** in west central Portugal is situated at 39°25'N; 09°15'W, 80 m a.s.l. The site corresponds to a field trial established to follow the above-ground biomass production of eucalypt and pine species, and includes four plots (50 m × 50 m) planted with Maritime (*Pinus pinaster* Ait.) pine and four planted with Monterey pine (*Pinus radiata* D. Don). Both plantations were 23 years old in 1990 and without any understorey (some low Ulex sp. bushes were removed in 1989). The site is situated on Cretaceous sandstones covered by Pleistocene sand. The soils are mostly Spodosols with a sandy texture. The clay content is lower than 5 per cent down to 60 cm depth. pH and the organic carbon content in the upper 15 cm layer vary, in the range 4.6 to 5.6 and 0.56 and 2.02 per cent, respectively. Annual mean temperature and precipitation are 15.2°C and 607 mm, respectively, the dry season from June to September having an average of less than 10 per cent of the annual precipitation. The climate is Mediterranean, tempered by oceanic influence. Climatic data refer to the nearest meteorological station "Caldas da Rainha" (1941-1970) situated at an altitude of 70 m a.s.l., 10 km from the site. In the present study two plots were used; 308:1 with a monoculture of Maritime pine and plot No 308:2, with a mixed culture of Maritime pine and Monterey pine in the proportions 1:1.

Site **Doñana (No 29)** in southwestern Spain at 38°07'N; 06°12'W and an altitude of 2 m a.s.l. is situated near the coastline in the Doñana National Park. The temperature is 16.6°C, and the mean annual precipitation 557 mm. The actual annual evapotranspiration is 479 mm and the potential annual evapotranspiration 871 mm. The site has a Stone pine (*Pinus pinea* L.) monoculture and the ground is without an understorey. The stand was about 44 years old (in 1990).

The site **Vallgorguina (No.313:MI)** is situated about 54 km north of Barcelona in northeast Spain (41°40'N; 02°30'E, 230 m a.s.l.). The annual mean precipitation is 736 mm and the annual mean temperature, 13.6°C. The forest, 18 years old (in 1991), is a Monterey pine monoculture with a sparse and low understorey of Holm oak (*Quercus ilex* L.), *Vitis* spp., *Rubus ulmifolius* and *Hedera helix* L. This plot was formerly a vineyard. The parent rock is granodiorite.

The site **Santa Coloma de Farners plot No. (314:MA)** is situated about 100 km northwest of Barcelona in northeast Spain (41°52'N; 02°33'E, 200 m a.s.l.). The annual mean precipitation is 750 mm and the annual mean temperature, 15.6°C. The forest, 22 years old (in 1991), is a Monterey pine monoculture with

a sparse and low understorey of Holm oak, *Vitis* spp., *Rubus ulmifolius* and *Hedera helix*. This plot was formerly used for growing sweet chestnut (*Castanea sativa* Mill.). The parent rock is granite.

Sites Nos. 2, 3, 100-108 and 10:1 have also been described by Johansson (1986). All site numbers below 109 are the same as those used by Berg et al. (1991).

A further 16 sites in Sweden, studied by A. Albrektson (1988), are included in this material. These sites are distributed between 56°N and 67°N (Albrektson, 1988; Fig 1) and are yield trials in Scots pine stands belonging to the Department of Forest Yield Research, Swedish University of Agricultural Sciences (Anon., 1974). Site descriptions are given in A. Albrektson (1988).

Fig 1. Map giving the approximate position of sampling sites for litterfall

MATERIALS AND METHODS

PLOT SIZE AND DESIGN

The size and shape of the plots varied: at site No. 2 plot size was 10 x 30 m; at site No. 6, (plots 6:51 and 6Ih4), it was 50 x 50 m; plots Nos. 313 and 314 measured 20 × 20 m; the other plots measured at least 40 × 40 m or covered a correspondingly large area.

SAMPLING METHOD

At all sites, circular litter traps were used, with a nominal sampling area of 0.25 m^2 cf. Newbould, (1967). Traps were mounted at a height of ca 1 m above ground. The Terylene net used had a mesh size of ca 1 mm. At sites Nos. 313 and 314, the nominal sampling area of each trap was 0.283 m^2. In the young stand at site 6Ih3, the sampling area of each trap was 0.0294 m^2 J.G.K. Flower-Ellis and L. Olsson (1978).

DISTRIBUTION PRINCIPLES FOR LITTER TRAPS

The litter traps were laid out randomly in all plots.

NUMBER OF REPLICATES

The number of replicate traps varied among the plots. Thus plot No. 6:51 (Ih 5) had 32 traps, No. 6:(Ih 4) 16 and No. 6:(Ih 3) had 32 traps initially, increased to 40 from September 1975, following inspection of the variance. Plots Nos. 300, 29, and 308 had 20 replicate litter traps. Plots Nos. 313 and 314 had 6 replicate traps and the other plots 10 replicate traps each.

SAMPLING FREQUENCY

The sampling frequency varied among the plots. At sites Nos. 2, 3, 100-108 and 10:1, traps were emptied three times a year, whereas at site No. 6, they were emptied 16-18 times during the snow-free period, i.e. at intervals of 7-14 days, depending on season. At plots Nos. 29, 300 and 308, traps were emptied 4, 5, and 6 times a year, respectively. At plots Nos. 313 and 314, traps were emptied 6 times a year.

TREATMENT OF SAMPLES

At site 6, samples were sorted into the following fractions: needles, bark, cones, twigs, branches and a fine fraction cf. J.G.K. Flower-Ellis and L. Olsson (1978). At the other sites, litter was sorted into two fractions: needles, and a composite fraction consisting of all the above components. The fractions were then dried separately. All material from all sites was dried at 85°C for 2 days. After drying, the fractions were weighed individually.

RESULTS AND DISCUSSION

COMMENTS TO THE SAMPLED FRACTIONS

The method used at all sites, namely the circular litter traps of 0.25 m^2, could be expected to give reliable values for needle litter, whereas cone and branch litter is less reliably sampled using that method. In no case could the amount of plate bark be estimated.

RESULTS FROM A LONG-TERM MEASUREMENT SERIES AT ONE SITE WITH SCOTS PINE

TRENDS IN TOTAL LITTERFALL

At the site Jädraås, litterfall was observed for seven years in three Scots pine stands, initially 18, 55 and 120 years of age. Sampling was discontinued in the youngest stand after the year 1979/80, but is still in progress in the two older stands cf. J.G.K. Flower-Ellis (1985). Some trends with time were evident within stands, and there were clear differences between them.

The series of observations revealed an increase in total litterfall in all three stands (Appendix 1). The increasing trend in litterfall in the young stand may be attributed, to some extent, to an increase with tree size in a stand which was 18 years old at the start of the study, and 25 years old when it ceased. A similar trend was observed in the two older stands, suggesting that a common (environmental) cause also underlay the increase. The marked decrease in total litterfall observed in the 55-year-old stand in the period 1973/74 to 1974/75 was reversed in 1976/77, to an increase which culminated in 1981/82 (Figure 2). The mean total litterfall in the period 1976/77 to 1982/83 was about 142 per cent of that in the first three years of the series cf. J.G.K. Flower-Ellis and L. Olsson (1978). A less marked increase in total litterfall appeared in the old stand a year later, but nevertheless lay, during the period 1977/78 to 1982/83, at 127 per cent of the mean for the early years of the series.

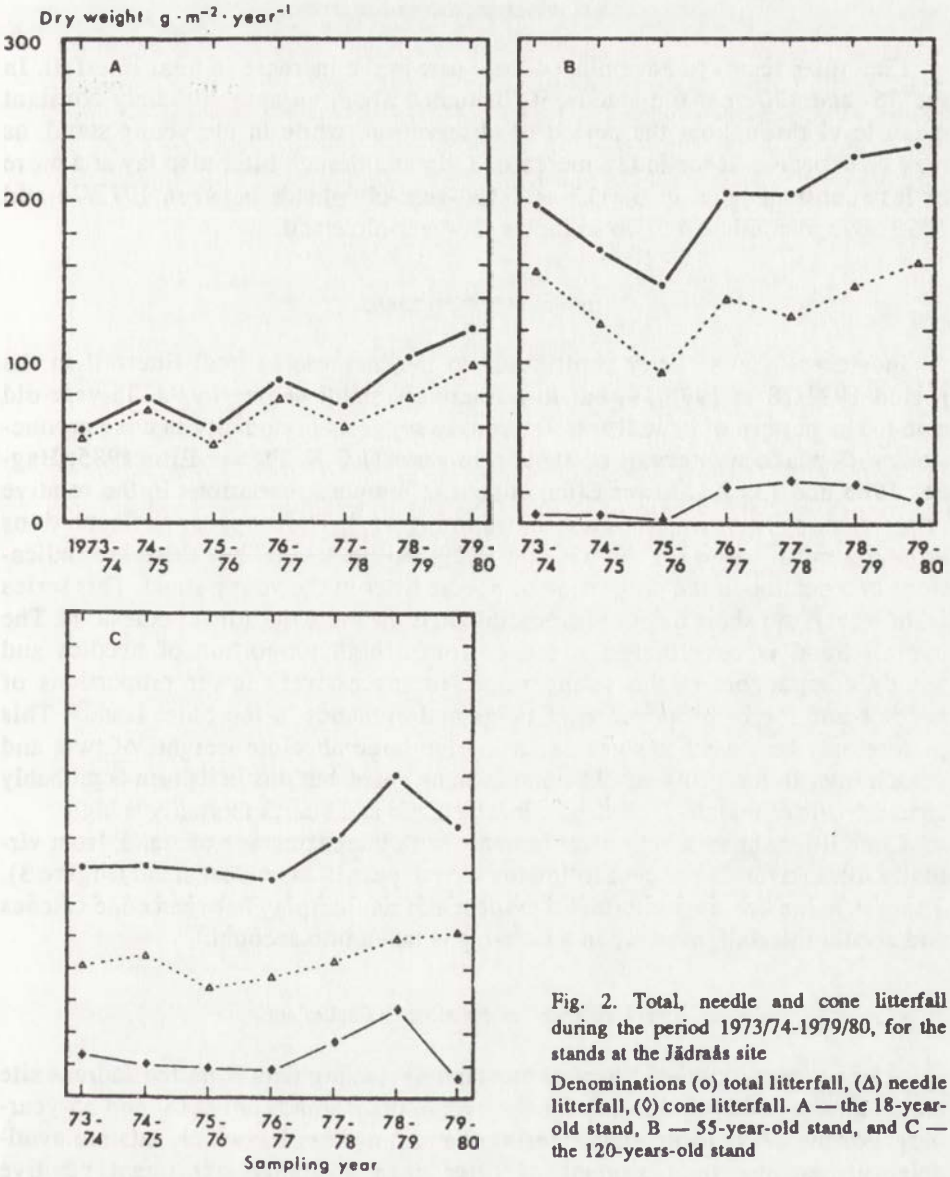

Fig. 2. Total, needle and cone litterfall during the period 1973/74-1979/80, for the stands at the Jädraås site

Denominations (o) total litterfall, (Δ) needle litterfall, (◊) cone litterfall. A — the 18-year-old stand, B — 55-year-old stand, and C — the 120-years-old stand

TRENDS IN NEEDLE LITTER

Much of the above increase in total litterfall can be attributed to increased needle litterfall (Appendix 1; Fig. 2). This showed a very similar course of change, especially in the 55- and 120-year-old stands. Needle litterfall in these two stands increased to 132 and 126 per cent, respectively, of the level during the period 1973/74 to 1975/76. The young stand also showed an increase in needle litter.

TRENDS IN FINE LITTER AND BRANCH LITTER

Fine litter seems to have played little part in the increase in total litterfall. In the 55- and 120-year-old stands, it fluctuated about an approximately constant mean level throughout the period of observation, while in the young stand, as may be expected, it tended to increase. Twig and branch litter also lay at a more or less constant level in the 55- and 120-year-old stands between 1973/74 and 1989/80, and continued to do so in the 120-year-old stand.

TRENDS IN CONE LITTERFALL

Increases in cone litter contributed to the increase in total litterfall in the period 1977/78 to 1978/79, but to a relatively small degree in the 55-year-old stand. The pattern of cone litterfall strongly suggests periodicity in cone production, with peaks at intervals of about five years (J.G.K. Flower-Ellis 1985; Hagner 1965 and J.G.K. Flower-Ellis, unpubl.). Temporal variations in the relative proportions of litter fractions are shown in Figure 3. These appear as fluctuations around a mean value for the 55- and 120-year-old stands, but there are indications of a decline in the proportion of needle litter in the young stand. This series is, however, too short for it to be possible to draw more definite conclusions. The overall trend is nevertheless evident; from a high proportion of needles and woody components in the young stand, to successively lower proportions of needles and larger proportions of twigs and branches in the older stands. This picture may be biased to some extent by the large absolute weights of twig and branch litter in the 120-year-old stand in some years, but this in its turn is probably characteristic of middle-aged stands, in which tree and branch mortality is high.

Cone litter shows a very clear increase with increasing age of stand, from virtually nil, to over 25 per cent following a cone year in the oldest stand (Figure 3). There is in the present material no evidence of an interplay between cone catches and needle litterfall, even when a time-lag is taken into account.

LINEAR RELATION FOR LITTERFALL VS STAND AGE

A linear regression of litterfall on stand age, using data from the Jädraås site alone, gave a good relationship for the two younger stands only (18- and 55-year-old). For the 18-year-old stand, during the seven years for which data are available, use of the total amount of litter gave a highly significant positive relationship. The 55-year-old stand also showed a significant, positive relationship for the ten years during which it was followed (Figure 2). This indicates that during the age interval concerned, the amount of litter was still increasing. However, this trend seems not to be an effect of age alone, but includes a temporal trend which is common to all three stands. The old stand did not fit satisfactorily into the overall picture. At an age of 120 years, it may no longer have been expanding its needle mass; but there was no indication that this was declining, during the period of observation.

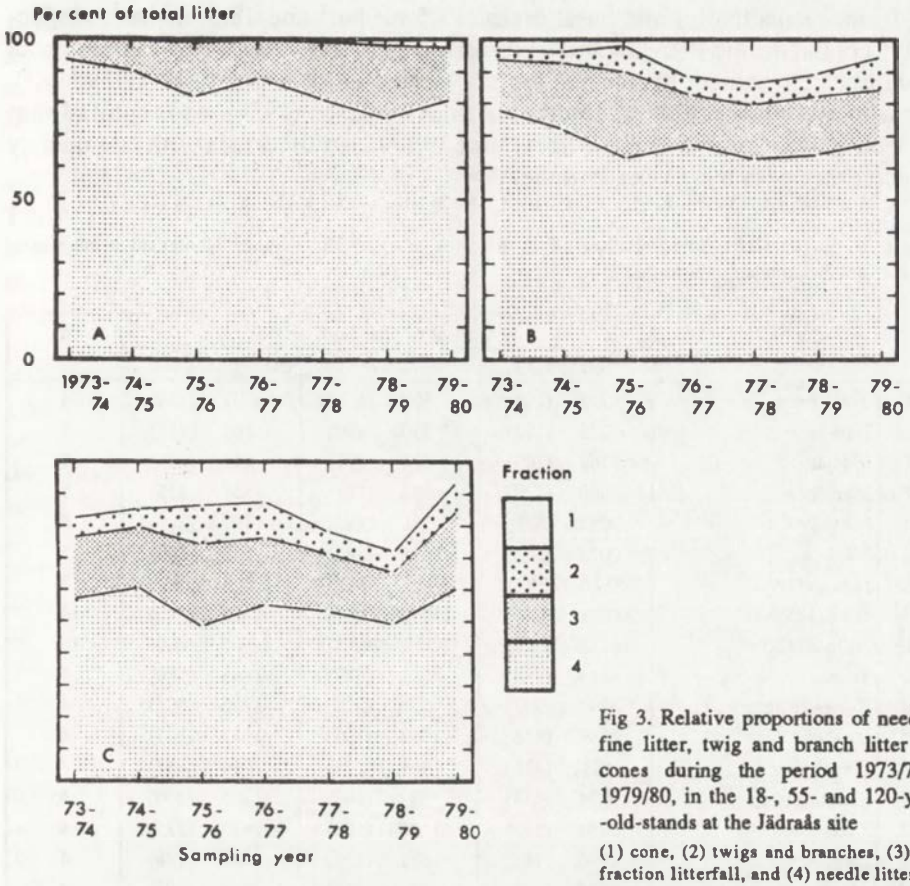

Fig 3. Relative proportions of needles, fine litter, twig and branch litter and cones during the period 1973/74 - 1979/80, in the 18-, 55- and 120-year--old-stands at the Jädraås site

(1) cone, (2) twigs and branches, (3) fine fraction litterfall, and (4) needle litterfall. A. the 18-year-old stand, B. the 55-year-old stand, and C. the 120-year-old stand

LITTERFALL IN A TRANSECT OF SCOTS PINE SITES ACROSS SCANDINAVIA

At 14 different sites litterfall was followed during three to five years (Table 2; Appendix 2). Three-year measurements were carried out at site No 105, four-year measurements at site Nos 100, 102, 103-104, 106-108 and 10:1 and at site Nos 2, 3:1, 3:2, 3:3 and 101 litterfall was measured during five years. The mean annual needle litterfall varied from 530 $kg \cdot ha^{-1}$ (site No 2) to 2312 $kg \cdot ha^{-1}$ (site No 102). The lowest amounts were found at nutrient-poor sites, generally with sediment soil, in the north. At more nutrient-rich sites with till deposits or clays, litterfall mass was higher. Among sites of similar fertility, needle litterfall was lower for sites situated in the north than for sites with a more southern situation. This is evident when needle litterfall at the two sites, No 100 (latitude 66°32'N) and 108 (latitude 58°07'N), are compared. These sites had nearly identical site index (17 m)

and 16 m, respectively) and basal areas (17.5 $m^2 \cdot ha^{-1}$ and 18.3 $m^2 \cdot ha^{-1}$, respectively) but the needle litterfall at the northern site (608 $kg \cdot ha^{-1}\ y^{-1}$) was only about one-third of the amount obtained at the site located in the south (1571 $kg \cdot ha^{-1}\ y^{-1}$). This is in accordance with the findings of A. Albrektson (1988) who reported that the needle litterfall in stands of Scots pine in Sweden increases with site quality but decreases with increasing latitude.

Table 2. Average values for total litterfall at the sites. n gives the number of measurement years. Standard deviation within paranthesis.

Site No.	Name	Amount of litter ($kg \cdot ha^{-1}$)			n
		Total (S.D.)	Needles (S.D.)	Other (S.D.)	
100	Skällarimsheden	915 (189)	608 (176)	307 (58)	4
2	Harads	735 (122)	530 (90)	205 (118)	5
3:1	Manjärv	1362 (209)	713 (71)	649 (176)	5
3:2	Manjärv	1680 (320)	913 (117)	767 (215)	5
3:3	Manjärv	2084 (333)	688 (85)	1397 (289)	5
101	Västbyn	2023 (352)	1476 (385)	547 (169)	5
6:Ih3	Jädraas (18 yr)[1]	829.6 (264.4)	694.8 (166.7)	134.8 (78.9)	7
6:Ih4	Jädraås (55 yr)[1]	2212.4 (494.5)	1505.5 (335.9)	706.8 (219.0)	10
6:51	Jadraås (120 yr)[1]	1621.5 (225.1)	935.0 (188.3)	633.1 (205.0)	10
102	Tomta	4198 (747)	2312 (429)	1886 (580)	4
103	Kungs-Husby	3997 (967)	2241 (513)	1756 (505)	4
104	Dimbo	3689 (356)	2002 (150)	1687 (247)	4
105	Grensholm	3881 (418)	1965 (276)	1916 (437)	3
106	Remningstorp	3284 (443)	1858 (148)	1326 (400)	4
107	Tveten	3034 (323)	1420 (157)	1615 (275)	4
108	Sänksjön	2096 (83)	1571 (125)	524 (88)	4
10:1	Mästocka	2096 (197)	1248 (66)	848 (203)	4
300	Roggebotzand	4436 (1052)	4402 (1044)	34 (15)	1
308:1	Furadouro	4568 (1071)	3395 (791)	1173 (629)	1
308:2	Furadouro	6182 (2281)	5005 (1294)	1177 (1217)	1
29	Doñana	2279 (846)	1211 (332)	1068 (582)	1
313	Vallgorguina	3169 (982)	2659 (793)	510	1
314	Santa Coloma de Famers	4016 (323)	3519 (236)	497	1

1. Measurements during the age period 18-25, 55-65, and 120-130 years resp.

The variation in needle litterfall between years was rather low. Ratios of maximum to minimum yearly needle litterfall ranged between 1.1 and 2.1, but for the majority of sites were less than 1.3. These ratios are much lower than J.R. Bray and E. Gorham (1964) found (up to 5.1 for gymnosperms) when reviewing a number of studies where litterfall has been monitored for over four years. During the period during which litterfall was sampled at the different sites (generally 1978-83 for stands in northern Sweden and 1979-83 for stands in Central and South Sweden), needle litterfall was lowest during the year 1979/80 at 12 of the 14 studied sites. Some of the sites situated in the south of Sweden (sites Nos 102,

105-107) showed a steady increase in needle litterfall during the period 1979/80 to 1981/82. The increase was generally rather small, about 120-130 per cent. At one site, however, it was more marked (site 102) and amounted to 150 per cent. During the last sampling year (1982/83), litterfall decreased again.

The fraction "other" which in this study consisted of fine litter, cones and small twigs, varied from 205 $kg \cdot ha^{-1}$ y^{-1} (site 2) to 1916 $kg \cdot ha^{-1}$ y^{-1} (site 105). The proportion of "other" material in the total litterfall when larger twigs and branches are excluded, varied between 25 per cent and 67 per cent in the stands studied. However, in most of the stands the "other" litter fraction accounted for about 40 to 50 per cent of the total annual litterfall. There was a tendency towards a lower proportion of "other" material in the total litterfall in older stands than in younger ones. In stands aged about 70 years and more (sites Nos 2, 100, 101 and 108) the "other" fraction accounted for between 25 per cent and 33 per cent of the total annual litterfall. This should not be interpreted as indicating that there is a larger proportion of needles in older stands, since the situation seems to be quite the opposite. The results obtained in the age series of Scots pine stands at the site Jädraås point to that. At that site, there was a successively lower proportion of needles and a larger proportions of twigs and branches in older stands. The tendency seen in the present study, towards a lower proportion of "other" material in total litter-fall in older stands may be due to the fact that larger twigs and branches were not included in the results. This, in turn, may be a consequence of the type of trap employed.

The mean annual total litterfall (larger twigs and branches excluded) varied from 735 $kg \cdot ha^{-1}$ (site 2) to 4198 $kg \cdot ha^{-1}$ (site 102). The proportion of needle material in the total litterfall, which comprises needles and fine litter, varied between 33 and 75 per cent in the stands studied. However, in most of the stands the needle litter fraction accounted for about 50 to 60 per cent of the total annual litterfall. According to C. Bonnevie-Svendsen and O. Gjems (1957) and E. Mälkönen (1974), needle litterfall is approximately 75 per cent of the total litterfall in Scots pine stands. Their values are higher than ours, despite the fact that larger twigs and branches are not included in our figures.

LITTERFALL AT SITES WITH AUSTRIAN PINE, STONE PINE, MARITIME PINE, MONTEREY PINE AND A MIXED PINE STAND

Litterfall values for the continental sites all cover a single year and the range of variation is therefore unknown. In all cases, the trapping method used allowed us to rely mainly on the needle litter values; therefore, only these have been used in the comparisons.

The continental sites all had relatively high litterfall values as compared to the Scots pine sites in Scandinavia (Table 2). The site at Furadouro, with a mixed culture of Maritime pine and Monterey pine, had a very high needle litterfall, with 5005 $g \cdot m^{-2}$ and a total litterfall of 6200 $g \cdot m^{-2}$. The monocultural stand of

Table 3. Simple and multiple linear regression for annual amounts of total litterfall and needle litterfall (kg ha^{-1}) as dependent on latitude, stand age, site index and basal area in Scots pine stands. Scandinavian transect plus three Jädraås sites. Levels of significance; 0.05- 0.01(*), 0.01-0.001 (**), < 0.001 (***)

	b (SE)		a (SE)		Sy.x	r^2	n
Simple linear regressions							
Total litter							
– latitude	-212.51	(67.58) **	15387.38	(4156.41)	915.60	0.39	17
– age	-19.28	(10.09) ns	3538.65	(702.68)	1057.60	0.19	17
– site index	153.40	(39.27) **	-1154.73	(916.39)	830.33	0.50	17
– basal area	102.68	(25.14) ***	132.71	(574.61)	811.51	0.52	17
Needle litter							
– latitude	-124.93	(32.32) **	9006.13	(1987.63)	437.84	0.49	17
– age	-7.37	(5.58) ns	1812.35	(389.02)	585.51	0.10	17
– site index	59.27	(24.93) *	-15.27	(581.85)	527.21	0.25	17
– basal area	55.88	(12.61) ***	134.17	(288.28)	407.14	0.56	17
Other litter							
– latitude	-87.57	(41.10) *	6381.23	(2527.95)	556.87	0.23	17
– age	-11.90	(5.22) *	1775.29	(263.98)	547.82	0.25	17
– site index	94.12	(17.68) ***	-1139.46	(412.74)	373.98	0.65	17
– basal area	46.80	(15.54) **	-1.46	(355.34)	501.83	0.37	17
Multiple linear regressions							
Total litter							
– latitude plus	-152.70	(50.61) **			653.92	0.71	17
basal area	83.39	(21.24) **	9924.33				
– site index plus	93.60	(42.26) *			722.84	0.64	17
basal area	66.63	(27.68) *	-1224.16				
– latitude plus	-130.86	(47.43) *			595.89	0.77	17
site index plus	70.47	(35.82) ns					
basal area	59.01	(22.98) *	7501.89				
Needle litter							
– site index plus	13.94	(24.35) ns			416.58	0.57	17
basal area	50.51	(15.95) ns	-67.90				
– latitude plus	-93.31	(21.03) ***			271.26	0.81	17
basal area	44.09	(8.82) ***	6117.27				
– latitude plus	-94.14	(22.42) **					
site index plus	-2.69	(16.93) ns					
basal area	45.03	(10.86) **	6209.75		281.68	0.82	17
Other litter							
– site index plus	79.66	(21.65) **					
basal area	16.11	(14.18) ns	-1156.26		370.41	0.68	17
– latitude plus	-59.39	(36.94) ns					
basal area	39.29	(15.50) *	3807.04		477.25	0.47	17
– latitude plus	-36.72	(28.86) ns					
site index plus	73.17	(21.79) **					
basal area	13.97	(13.98) ns	1292.55		362.48	0.71	17

Maritime pine at the same site had a needle litterfall of 3400 $g \cdot m^{-2}$. The stands had the same age, 24 years.

The sites Vallgorguina and Santa Coloma de Farners, both with Monterey pine, had a needle litterfall of 2660 and 3529 $g \cdot m^{-2}$, respectively. The site Doñana, with a Stone pine monoculture, had a needle litterfall of 1210 $g \cdot m^{-2}$ and a total litterfall of 2280 $g \cdot m^{-2}$. A stand of Austrian pine at Roggebotzand had a relatively high litterfall of 4400 $g \cdot m^{-2}$, which was very close to the total litterfall of 4440 $g \cdot m^{-2}$.

LINEAR RELATIONS OF LITTERFALL IN SCANDINAVIA TO STAND AGE, LATITUDE, BASAL AREA, AND SITE INDEX

LITTERFALL VS STAND AGE

In his study A. Albrektson (1988) could relate annual amounts of needle litterfall to stand age in a transect across Scandinavia, with an r^2 value of 0.46. Also site index gave a clear and good relation (r^2=0.65). In his study, A. Albrektson found site index to be superior as a predictor of litterfall.

In the present paper we have attempted to make similar correlations using data from the transect of M.B. Johansson (1986) (Appendix 2) here called the "Scandianavian transect" to distinguish it from that of A. Albrektson (1988) and from long-term studies in an age series at the site Jädraås (Appendix 1). In an attempt to construct a regional model we began by using the data of the Scandinavian transect plus those of the Jädraås site, and comparisons were made between annual total litterfall and needle litter, and stand age, basal area, site index and latitude, using available data (Table 3). We later included data from the transect of A. Albrektson in our analysis. This, on the other hand gave an r^2 value of 0.10 (n=33; ns) (Table 4).

LITTERFALL VS LATITUDE

By using the data of the Scandinavian transect plus the Jädraås site, we obtained a negative relationship between latitude and litterfall (both total litterfall with r^2=0.39; n=17; $p < 0.01$and needle litterfall with r^2=0.49; n=17; $p < 0.01$) (Table 3). This may be compared with the results of A. Albrektson (1988), who also found a negative relationship (r^2=0.46; n=16). When all Scots pine data were combined, and a regression calculated between annual needle litterfall an r^2 value of 0.48 was obtained, a relationship that could be regarded as stable (Fig. 4).

LITTERFALL VS BASAL AREA

For the data from the Scandinavian transect, basal area gave a coefficient of determination (r^2) of 0.56 for needle litterfall (n=17). Total litterfall gave a somewhat less good relationship (r^2=0.52) and "other litter" gave a not as good fit (r^2=0.37; Table 3). When all available data from 33 sites were combined (Table

4), basal area gave a highly significant, still poorer relationship with needle litterfall (Figure 5; r^2=0.26; n=33; $p < 0.01$).

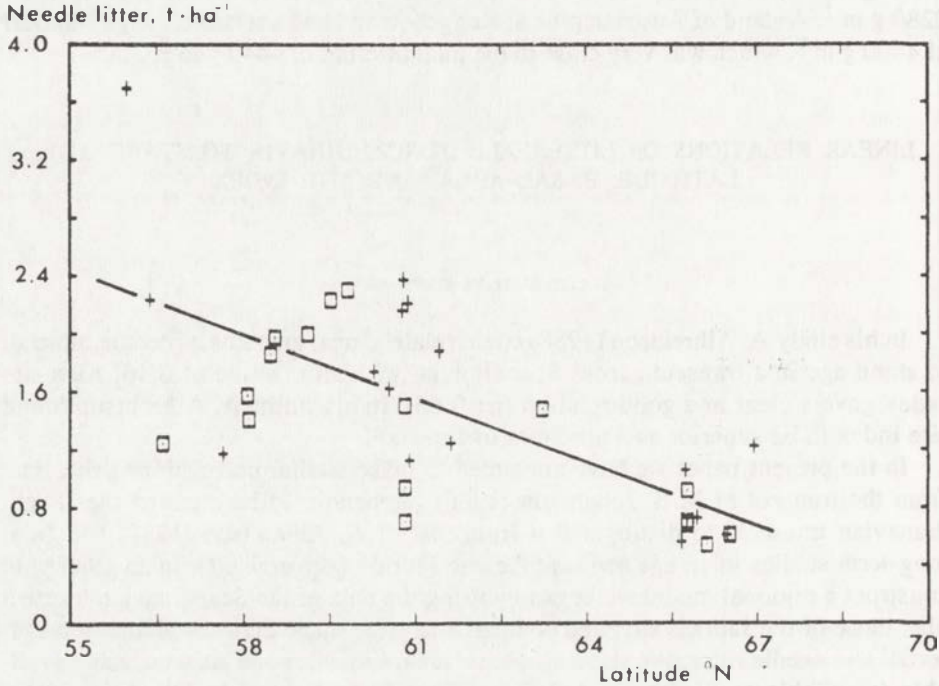

Fig 4. Needle litterfall for Scots pine as compared to latitude

(□) Scandinavian transect incl. data from the Jädraås site, (+) data taken from A. Albrektson (1988). r^2=0.48; n=33; $p < 0.001$.

LITTERFALL VS SITE INDEX

Site index values were available for the Scandinavian transect, the transect of A. Albrektson (1988) and for the Jädraås site. For the Scandinavian transect plus data from the Jädraås transect, site index gave an r^2-value of 0.50 (n=17) for total litterfall and 0.27 for needle litterfall (Table 3). The A. Albrektson transect gave an r^2 value of 0.65 (n=16). When the data for these two transects were combined with those for the Jädraås site, we obtained an r^2-value of 0.42 (n=33 $p < 0.001$; Table 4; Figure 6).

Table 4. Simple and multiple linear regression for average annual amounts of needle litterfall (kg·ha^{-1}) as dependent on latitude, stand age, site index and basal area in Scots pine stands in Scandinavia. All available average values for Scots pine were used (Appendices 1 and 2; A> Albrektson, 1988). Levels osfsignificance; 0.05-0.01 (*), .0.01-0.001(**), < 0.001 (***)

	b (SE)		a (SE)		Sy.x	r^2	n
Simple linear regression							
Latitude	-147.16	(27.02) ***	10526.81	(1666.66)	519.11	0.48	33
Site index	93.49	(19.35) ***	-676.41	(453.65)	548.48	0.42	33
Age	-9.01	(2.62) **	2105.20	(215.27)	618.11	0.27	33
Basal area	46.32	(13.69) **	281.91	(366.09)	620.48	0.26	33
Multiple linear regression							
Site index plus	75.55	(20.51) ***	-924.01		523.44	0,49	33
basal area	25.77	(12.82) ***					
Latitude plus	-140.60	(20.59) ***	9030.30		394.30	0.71	33
basal area	42.42	(8.72) ***					
Latitude plus	-122.17	(24.23) ***	7487.37		388.67	0.73	33
site index plus	25.31	(18.20) ns					
basal area	36.05	(9.74) ***					
Age plus	-4.54	(2.18)	8710.80		462.61	0.62	33
altitude plus	-2.07	(0.88)					
latitude	-107.51	(27.53)					

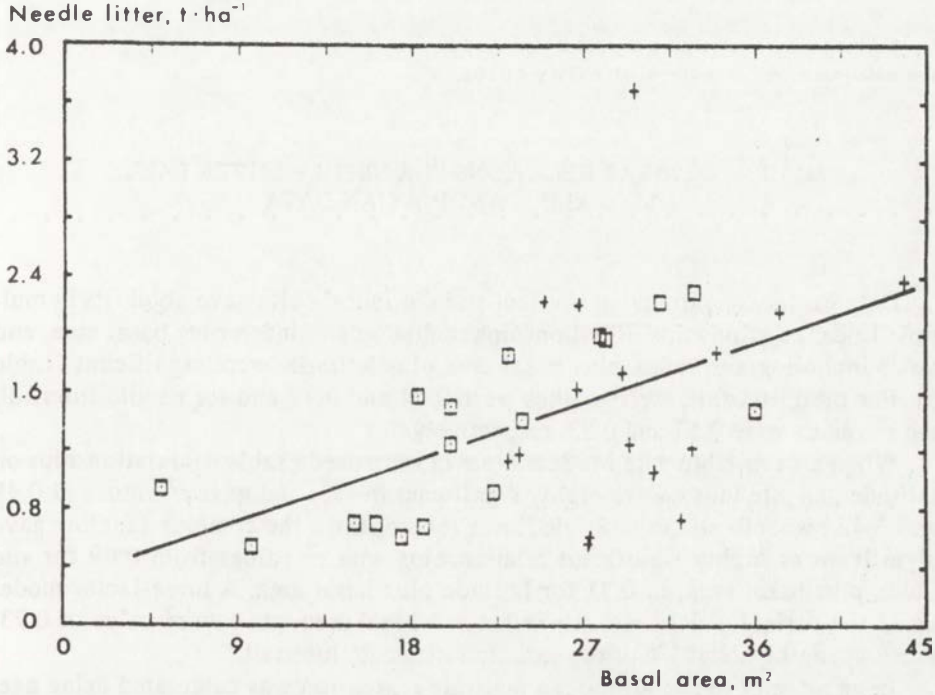

Fig . 5. Needle litterfall for Scots pine as compared to basal area
Denominations as in Figure 4. r^2=0.26; n=33; p < 0.01

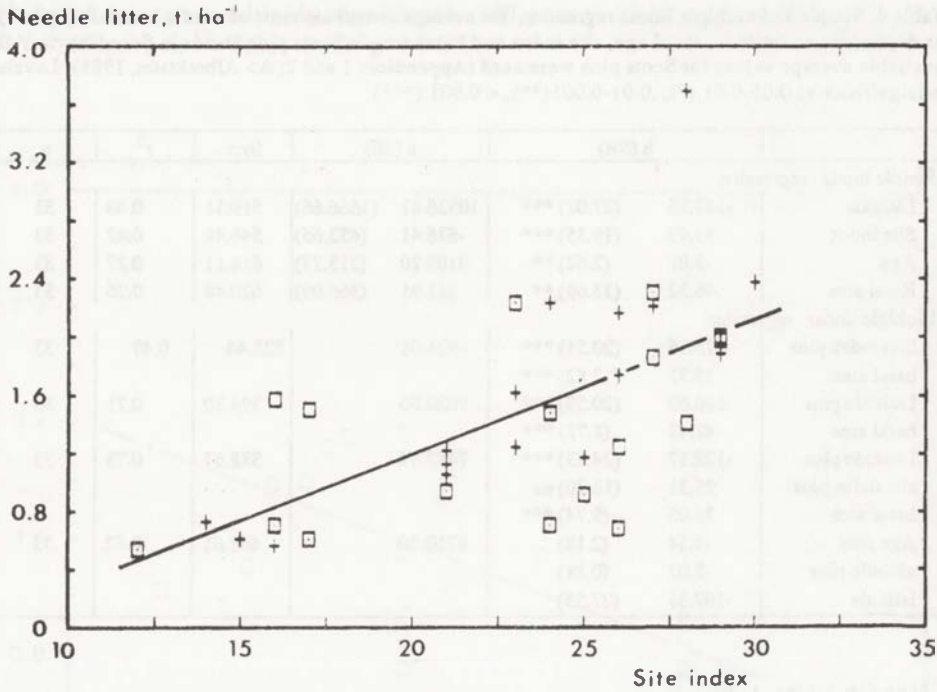

Fig. 6. Litterfall for Scots pine as compared to site index
Denominations as in Figure 4. r^2=0.42; n=33; p < 0.001.

MULTIPLE LINEAR RELATIONS FOR NEEDLE LITTER FALL, USING ALL SCANDINAVIAN DATA

Data for the Scandinavian transect and the Jädraås site gave good fits in multiple linear relationships. Relationships including site index plus basal area, and those including site index plus basal area plus latitude, were significant (Table 3). For total litterfall, the r^2 values were 0.64 and 0.77 and for needle litterfall, the r^2 values were 0.57 and 0.82, respectively.

When all available data for Scandinavia were used (Table 4), relationships on latitude and site index were highly significant (n=33) and gave r^2 values of 0.48 and 0.42 respectively. In multiple linear relationships the combined factors gave significant or highly significant relationships with r^2 values from 0.49 for site index plus basal area, to 0.71 for latitude plus basal area. A three-factor model using the variables, latitude, site index and basal area, gave an r^2 value of 0.73, thus explaining about 3/4 of the variation in needle litterfall.

In an attempt to use altitude, a multiple regression was calculated using age, altitude and latitude, resulting in an r^2 value of 0.62 (cf. the corresponding calculation for all European data, below).

LINEAR RELATIONS USING ALL THE EUROPEAN DATA

Having found what appeared to be suitable models for litterfall in Scots pine systems in Scandinavia we tried to generalize the results (Table 5). Assuming that the genus Pinus shares common characteristics with respect to litterfall, we combined the litterfall values for the species Austrian pine, Monterey pine, Maritime pine and Stone pine with those of Scots pine to obtain a transect from the Arctic Circle to the Mediterranean and including five pine species. A linear relation to latitude (Figure 8) gave a highly significant relationship as did a linear relation to stand age (Figure 7). A multiple linear regression was calculated using age, altitude and latitude, giving an r^2 value of 0.55, thus explaining about half of the variation (Table 5).

Table 5. Simple and multiple linear relations for average annual amounts of needle litterfall (kg ha^{-1}) as dependent on latitude, stand age, site index and basal area for stands of different pine species over western Europe. All available average values for Scots pine, Austrian pine, Maritime pine, Monterey pine and Stone pine were used (Table 3; Albrektson, 1988). Levels os significance; 0.05-0.01 (*), 0.01-0.001 (**), < 0.001 (***)

	b (SE)		a (SE)		Sy.x	r^2	n
Simple linear relations							
Latitude	-93.41	(17.60) ***	7251.19	(1043.43)	817.92	0.43	39
Multiple linear relations[1]							
Age plus	-7.22	(3.13) *	6178.67		692.63	0.55	38
altitude plus	-1.74	(1.22) ns					
latitude	-64.01	(3.66) ***					

1. The site No 300 (Roggebotzand) excluded as no site index was available.

CONCLUDING REMARKS

For Scandinavia, with only Scots pine, simple linear regressions gave good fits with latitude and site index, giving the most clear relationships and r^2 values of 0.48 and 0.42 respectively. In a multiple regression, latitude plus basal area gave an r^2 value of 0.71, a value that was not improved by site index.

The behaviour of the relationships changed when the continental sites were included in the analysis and even if the linearity still was good over a range in latitude from 38°N to 66°N and over five pine species we can not exclude that other patterns than linear ones will give a more correct picture.

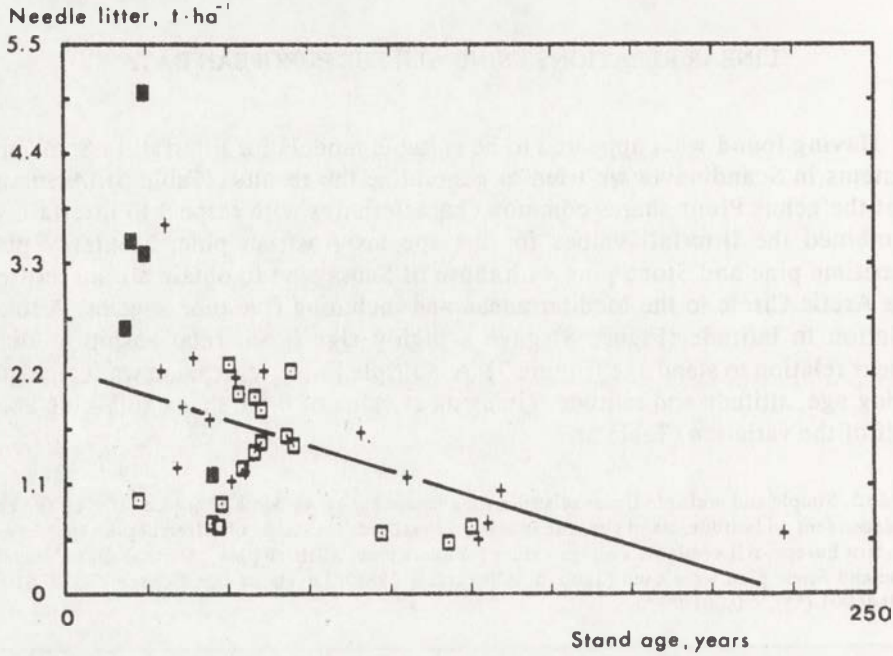

Fig. 7. Needle litterfall for Scots pine, Maritime pine, Stone pine and Monterey pine as compared to stand age (□) Scandinavian transect including data from the Jädrås site, (+) data taken from A. Albrektson (1988), (■) data from continental Europe, r^2=0.43; n=38; p < 0.001

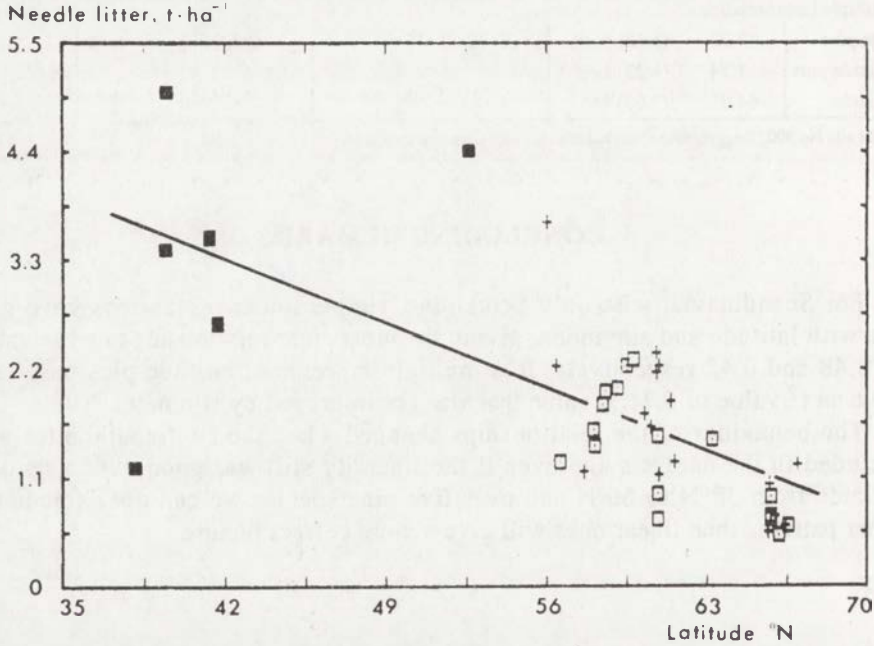

Fig 8. Needle litterfall for Scots pine, Austrian pine, Maritime pine, Stone pine and Monterey pine as compared to latitude

Denominations as in Figure 7. r^2=0.43; n=39; p<0.001

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APPENDIX 1

Variation in amounts in litterfall at different stand ages of Scots pine (*Pinus sylvestris*) at the Jädraås site (J.G.K. Flower-Ellis, 1985). The stand ages were 18, 55 and 120 years in 1973

Stand	Fraction (kg ha^{-1})					Collection year
	Total	Needles	Twigs	Fine	Cones	
Jädraås 18yr	585.6	549.8	1.6	34.2	0	1973/74
"	779.6	703.1	0.7	75.7	0	1974/75
"	590.6	484.2	5.4	100.9	0	1975/76
"	885.2	777.2	0.7	107.2	0	1976/76
"	735.1	598.8	2.4	133.9	0	1977/78
"	1027.7	774.9	17.6	235.2	0	1978/79
"	1203.7	975.5	30.1	198.0	0	1979/80
Mean value;	829.8	694.8	8.4	134.8	0	
S. D.	(264.4)	(166.7)	(10.5)	(78.9)	(-)	
Järaås 55 yr	1974.4	1546.5	59.3	307.9	60.5	1973/74
"	1699.0	1233.5	58.5	347.5	58.4	1974/75
"	1467.8	927.1	112.5	401.0	27.1	1975/76
"	2046.0	1379.5	105.3	328.5	232.4	1976/77
"	2037.6	1284.4	134.1	344.3	274.6	1977/78
"	2270.0	1455.7	151.0	417.1	246.2	1978/79
"	2339.6	1600.9	242.5	369.2	126.8	1979/80
"	2788.2	1703.8	662.0	375.5	46.7	1980/81
"	3161.3	2153.6	555.8	415.0	36.8	1981/82
"	2340.8	1769.7	111.6	341.9	117.5	1982/83
Mean value;	2212.4	1505.5	219.3	364.8	122.7	
S. D.	(494.5)	(335.9)	(202.3)	(35.4)	(89.8)	
Jädraås 120 yr	1419.9	811.3	89.4	273.3	245.7	1973/74
"	1428.7	865.6	86.4	273.7	202.9	1974/75
"	1399.8	682.8	175.8	357.9	183.6	1975/76
"	1335.1	737.2	144.9	289.2	163.6	1976/77
"	1602.0	851.9	114.6	290.2	345.0	1977/78
"	1985.1	976.6	129.9	327.0	551.5	1978/79
"	1681.4	1015.7	150.7	405.0	109.9	1979/80
"	1698.1	1076.4	193.8	301.7	126.1	1980/81
"	1921.7	1330.9	102.3	321.6	166.8	1981/82
"	1743.4	1001.5	126.7	355.4	259.6	1982/83
Mean value;	1621.5	935.0	121.5	319.5	235.5	
S. D.	(225.1)	(188.3)	(42.0)	(40.6)	(124.1)	

APPENDIX 2

Annual amounts of litterfall collected in a climatic transect across Scandinavia and at six sites on the continent

Site/year	Amount (kg ha^{-1})			
	Total	(S.D.)	Needles	(S.D.)
100 Skällarimsheden				
1979/80	997.9	(233.5)	624.5	(132.4)
1980/81	1134.1	(178.4)	823.8	(131.3)
1981/82	706.7	(118.0)	394.9	(51.7)
1982/83	820.7	(149.2)	587.9	(86.0)
2 Harads				
1978/79	905.3	(372.1)	491.1	(74.8)
1979/80	774.5	(209.0)	635.3	(120.9)
1980/81	595.4	(103.6)	440.2	(75.8)
1981/82	759.7	(156.6)	616.8	(98.7)
1982/82	639.1	(135.8)	467.4	(57.2)
3:1 Manjärv				
1978/79	1521.3	(338.8)	837.4	(176.4)
1979/80	1080.5	(345.4)	662.0	(209.9)
1980/81	1578.5	(429.3)	699.8	(133.1)
1981/82	1218.3	(315.1)	677.4	(125.8)
1982/83	1409.9	(233.1)	686.4	(133.3)
3:2 Manjärv				
1978/79	2196.2	(551.0)	1090.2	(169.9)
1979/80	1398.3	(216.2)	763.1	(139.3)
1980/81	1550.5	(285.6)	898.3	(136.0)
1981/82	1484.9	(257.3)	897.7	(110.4)
1982/83	1772.4	(325.3)	916.3	(185.2)
3:3 Majärv				
1978/79	2511.6	(472.1)	824.8	(250.0)
1979/80	1745.1	(271.7)	620.8	(223.5)
1980/81	1963.6	(323.6)	635.1	(196.8)
1981/82	1844.3	(295.6)	713.2	(230.4)
1982/83	2356.3	(243.3)	644.1	(242.2)
101 Västbyn				
1978/79	2091.6	(269.4)	1721.8	(189.4)
1979/80	1472.0	(288.7)	958.1	(171.2)
1980/81	2110.4	(283.4)	1282.1	(180.0)
1981/82	2446.2	(349.9)	1952.7	(214.9)
1982/83	1994.8	(360.6)	1467.7	(196.4)
6 Jädraås (see Appendix No. 1)				
102 Tomta				
1979/80	3252.3	(420.4)	1911.2	(488.1)
1980/81	5078.5	(762.6)	2557.1	(700.8)
1981/82	4240.8	(501.2)	2789.3	(443.2)
1982/83	4220.2	(486.1)	1990.4	(539.2)

Site/year	Amount (kg ha^{-1})			
	Total	(S.D.)	Needles	(S.D.)
103 Kungs-Husby				
1979/80	2956.8	(684.8)	1814.2	(398.2)
1980/81	5281.3	(1110.3)	2980.8	(506.3)
1981/82	3731.3	(966.6)	2154.4	(399.0)
1982/83	4018.9	(1069.3)	2014.9	(431.9)
104 Dimbo				
1979/80	3316.2	(929.0)	1882.4	(419.2)
1980/81	4057.6	(1046.0)	2046.3	(302.1)
1981/82	3460.7	(861.8)	1883.8	(316.8)
1982/83	3919.9	(885.4)	2195.0	(316.8)
105 Grensholm				
1979/80	3931.0	(1281.0)	1667.1	(485.2)
1980/81	3440.5	(880.8)	2015.4	(518.9)
1981/82	4271.4	(1116.6)	2211.9	(523.6)
106 Remningstorp				
1979/80	2673.0	(579.8)	1689.4	(327.2)
1980/81	3682.3	(934.0)	1809.0	(297.5)
1981/82	3259.3	(613.7)	2041.5	(358.1)
1982/83	3521.4	(570.1)	1893.1	(294.4)
107 Tveten				
1979/80	2680.4	(606.9)	1195.8	(131.4)
1980/81	3298.8	(653.8)	1435.6	(198.3)
1981/82	2841.2	(721.4)	1551.3	(299.0)
1982/83	3316.9	(541.1)	1496.4	(269.8)
108 Sänksjön				
1979/80	2974.0	(429.9)	1418.4	(316.2)
1980/81	2025.0	(471.8)	1561.0	(410.3)
1981/82	2067.8	(458.4)	1582.7	(420.5)
1982/83	2215.7	(668.4)	1723.2	(596.5)
10:1 Mästocka				
1979/80	2262.5	(867.9)	1173.7	(417.2)
1980/81	2267.1	(784.9)	1332.6	(448.8)
1981/82	1889.5	(541.4)	1254.4	(340.1)
1982/83	1964.7	(385.6)	1230.1	(268.5)
300 Roggebotzand				
1988/90	4436	(1052)	4402	(1044)
308:1 Furadouro				
1988/89	4568	(1071)	3395	(791)
308:2 Furadouro				
1988/89	6182	(2281)	5005	(1294)
29 Doñana				
1988/89	2279	(846)	1211	(332)
313 Vallgorguina				
	3169	(982)	2659	(793)
314 Santa Coloma de Farners				
	4016	(323)	3519	(236)

PRODUCTION/DECOMPOSITION OF ORGANIC MATTER IN FOREST; STUDIES IN ONE CLIMATIC REGION AND IN CLIMATIC GRADIENT

ALICJA BREYMEYER

Abstract . Production and decomposition of litter were studied in 12 coniferous and mixed forest standas: 6 stands located in one climatic region in Eastern Poland and 6 stands located on climatic transect from Northern Sweden to Central Poland. The rates of both process were evaluated by the same methods; much more detailed studies were carried out in Eastern Poland, especially various time spans were applied for evaluation of fall and decomposition rates. It was found, that production/decomposition budgets are diversified in both studies; under the influence of local microclimates and local soil conditions the processes of litter fall and litter decomposition change independently. Similarly, under the influence of different macroclimate the fall/decomposition processes rates are modified independently.

Key words: production/decomposition, forests, litter, organic matter

INTRODUCTION

The main task of this paper is the evaluation and analysis of two processes conditioning the budget of organic matter in forest ecosystems: falling of organic fragments onto forest bottom and decomposition of that matter.

Litter fall is one of the best known indices of organic matter production. This index is based on the simple and obvious assumption that anything that has been produced as live tissue must after some time die and falls down — this is organic fall or litter fall.

It is assumed that in forest ecosystems this constitutes a good comparative measurement of total productivity, although some data indicate that in case of passing to very high productivities the correlation of total production and litter fall becomes looser (Fig. 1). However, due to an enormous work-consuming character of direct evaluations of organic matter production in forests, use is being made of measurements of organic fall as a production measure, particularly for monitoring programmes (Breymeyer 1981) or for modelling (Ajtay, Ketner and Duvigneaud 1979). Theoretically it should be assumed that the whole organic mass produced within the ecosystem after some time dies and falls to the ground: an error of this evaluation is constituted by overlooking biomass losses due to consumption of various herbivorous organisms — a part of the produced plant mass is being eaten before it falls. This is an error, which in the case of forest ecosystems may be well ignored: according to evaluations of various authors the

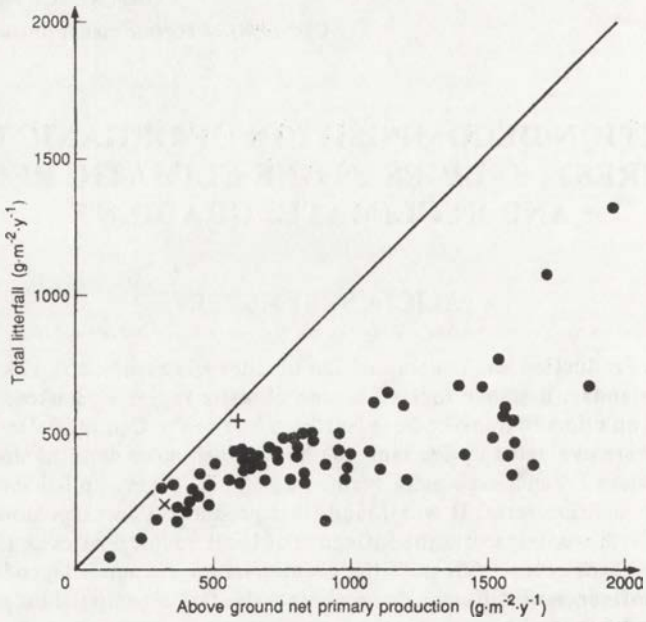

Fig.1. Annual litterfall as a function of primary production (ABVG NPP). Solid line marks the hypothetical 100% litterfall. After O'Neill and DeAngelis 1986; Debazac 1986; Grodziński, Weiner, Maycock 1984

consumption of herbivores in forests does not exceed a few percent. Thus organic fall, a measurement of "green annual production" of the forest, may be considered a good index of total aboveground production in forests. Measurements of productivity conducted in four pine-mixed forests, studied in great detail in Poland and in the USA, gave the following proportions (according to Rieger et al. 1984, Whittaker and Marks 1975):

Production of trees t.dw. $ha^{-1} \cdot y^{-1}$	2.5	4.7	7.9	14.3
including in per cent:				
trunks	53.2	61.0	22.0	21.9
leaves, fruit, twigs (litter)	40.4	53.7	24.7	57.4

As may be seen from this measurement about 25-50% of the aboveground forest production falls yearly to the ground: in the years when cones are produced this is a much higher percentage.

Dependence of organic fall on climate has been presented on Figure 2. There are numerous measurements; as distance from equator increases, the amount of organic matter supplied to the ground in various forests decreases, and this dependence is clear in gradient from parallel 0° to 70°. However, if the range is decreased and we limit ourselves to the area of Poland, changeability of the analysed measurements is chaotic, they do not show any correlations with latitude (Poland is situated between parallels 49 and 55° N, this is 6° of range). If one were to conduct an exercise

and study what shifts to the south-north are necessary in order to observe a regular changeability of organic fall, it seems that indispensable would be a step by about 20°. Does this mean that the total production of those ecosystems reacts to changeability of macroclimate only on areas embracing 20°?

Decomposition is one of the more significant processes regulating circulation and storage of matter and of basic edaphic components conditioning feeding of plants in natural terrestrial ecosystems, including also in forests. The rate of litter decomposition depends on local climate, structure of litter and the upper soil layer, as well as on activity of soil fauna and flora. Of basic significance are also characteristic traits of the freshly fallen litter material itself, mainly its chemical contents.

A lively discussion was and still is being aroused by dependence of litter decomposition rate and the contents of lignin in it. The first calculations carried out on measurements taken in forests of the temperate zone seemed to suggest that the lignin contents enables a very precise foreseeing of the time of litter decomposition, perfect correlations of both parameters have been indicated on still newer materials (Meentemeyer 1984). The universal character of this correlation was discarded when efforts were undertaken at applying it in extremely dry environments: in shrubby desert ecosystems no dependence was ascertained of the decomposition rate of plant remnants on their lignin contents (Schaefer, Steiberger and Whitford 1985). B. Berg (1986) suggests that in various stages the litter decomposition is being controlled by various factors, there are "lignin controlled" stages (controlled by the lignin contents), but also "nitrogen and phosphorus controlled" ones (dependent on the contents of nitrogen and phosphorus in litter falling to the forest bottom).

Among the more important features of the soil, considered as environment where the whole decomposition process progresses, are the chemical and physical characteristics and climate of the soil. Results of laboratory studies confirm a clear connection between temperature and humidity of upper soil horizons and their biological activity measured by the amount of freed carbon dioxide.

Studies on the influence of climatic factors on the litter decomposition have been conducted on a local scale by P.E. Jansson and B. Berg (1985). They have correlated the litter decomposition rate with properties of soil climate in forests of middle and southern Sweden. They have ascertained that the dynamics of decomposition may even in 85% be explained by changes in temperature and humidity. Such studies have also been conducted on a regional scale. According to V. Meentemeyer and B. Berg (1986) the spatial changeability of the decomposition rate in pine forests of Western and Northern Europe may in 77% be explained by changes in actual evapotranspiration.

In first part of this elaboration we have assumed that all stands of the studied forests are situated on an area similarly conditioned by macroclimate, and differences in the rate of fall and decomposition of litter depend on differentiation of soils, its vegetation cover and seasonal climatic changes.

In the second part of the elaboration we consider the dependence of both

studied processes on macroclimate and we analyse results of studies conducted on long North-South transect.

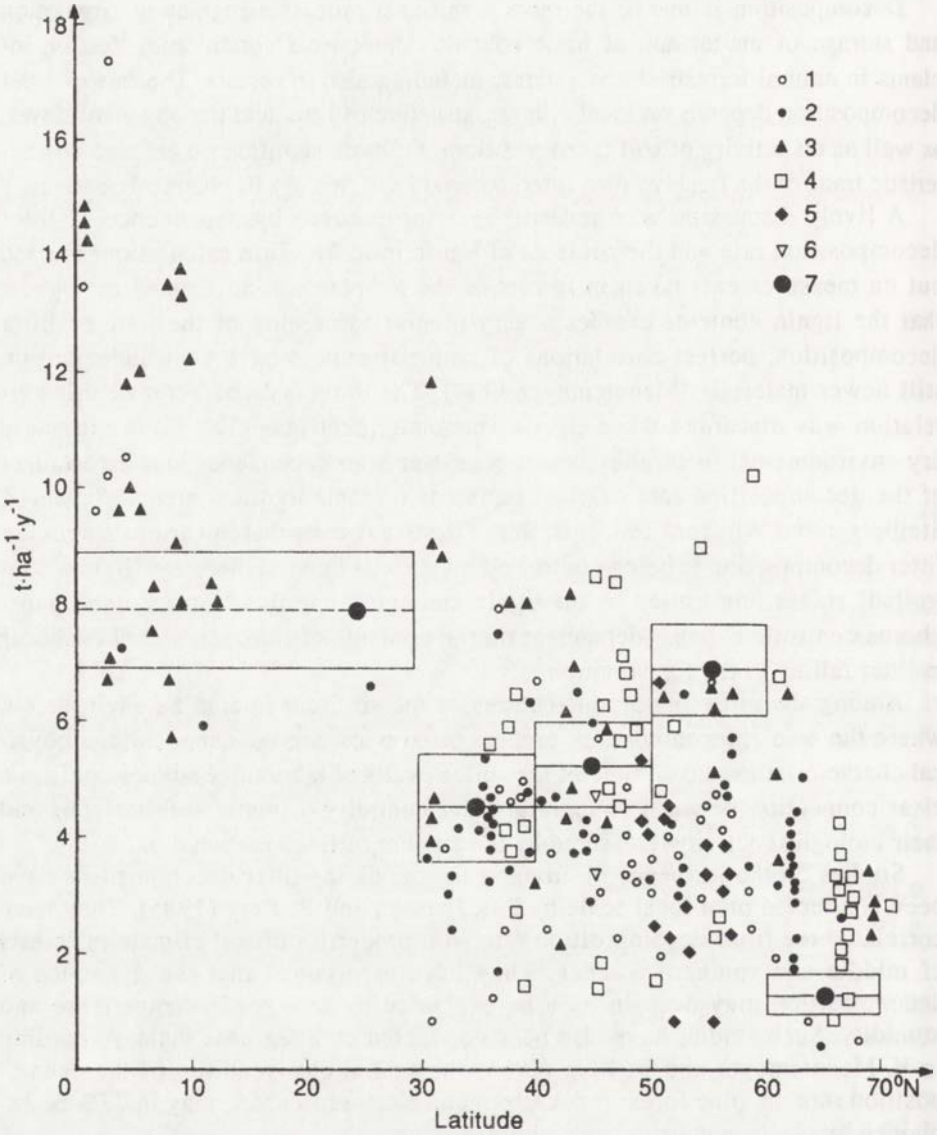

Fig.2. Annual litterfall as a function of latitude

1 – Bray and Gorham 1984; 2 – IBP Data Bank after Reichle 1981; 3 – Vogt and Co 1986, broadleaved forest; 4 – Vogt and Co 1986, coniferous forest; 5 – Breymeyer and Co unpublished data from coniferous and mixed forests; 6 – Alvera 1980. Measurements of wood production (means and standard deviations) after IBP Data Bank; 7 – Vogt and Co collection from both hemispheres remaining measurements from northern hemisphere

I. DETAILED STUDIES OF LITTER PRODUCTION-DECOMPOSITION IN FORESTS OF EASTERN POLAND

AREA AND STANDS OF STUDIES

Studies have been conducted in forest of Mierzwice and Litewniki villages, belonging to a large complex of on Bug River Forests about 20 km to the north of the town Biała Podlaska (Fig.3). Selected for studies were 6 stands representing types of forest biocenoses characteristic for that area. Efforts were undertaken to ensure that they should have a similar density of the tree layer and age of about 40 years. This enabled observing the differentiation of the rate of production-decomposition of litter depending on soil type, type of forest community and share of coniferous and boadleaved trees.

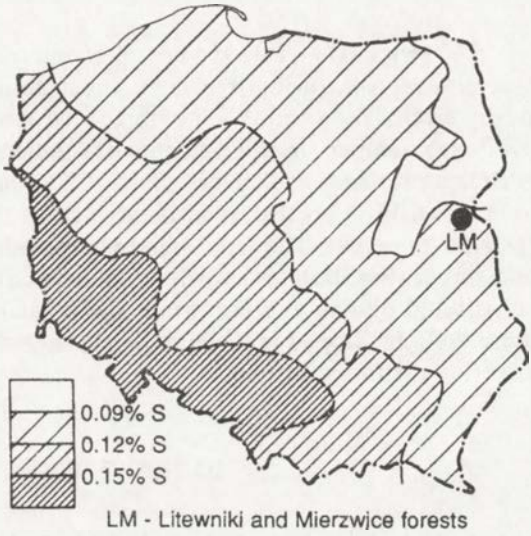

Fig.3. Litewniki and Mierzwice forest complexes marked on the map of pollution of Poland. Three zones of pollution are settled on the basis of measurements of sulphur content in pine needles (after Molski and Dmuchowski 1986)

In accordance with unanimous opinions and measurements of J. Wawrzoniak at al. (1988) and J. Juda at al. (1992) this part of Poland is outside the range of main air pollution brought over the area from industrial basins on the south-western part of the country. J. Wawrzoniak at al. (1988) indicate the surprisingly high winter pollution of air with nitrogen oxides; the authors relate this to the fact of a frequent usage of wood for warming dwellings in the north-eastern Poland.

Two forest complexes and stands have been selected in co-operation with the Centre for Studies and Control of Environment in Biała Podlaska. The stands are situated at a distance of 10-12 km from each other. Descriptions of stands in accordance with a phyto-sociological classification have been presented below.

PINE FORESTS

Mierzwice II — area grown over with pine forests classified as dry pine forest (*Cladonio-Pinetum*). In the layer of trees only the pine occurs (*Pinus sil-*

vestris), and the canopy coverage amounts 65-70%. Shrubs are represented by rare junipers (*Juniperus comunis*) and oak undergrowth (*Quercus robur*). The herb layer is constituted by a dense cover of moss and lichen.

Litewniki III — in the tree stand dominating is the pine, and it is accompanied by small quantities of birch and hornbeam. The forest has been classified to the complex of fresh pine forest (*Peucedano-Pinetum*). The canopy coverage amounts to about 75%. The undergrowth is very poorly developed and is comprised by oak and hornbeam. Herb layer dense, covering 80-85% of surface.

MIXED FORESTS

Mierzwice III — this is a complex of a relatively fertile fresh mixed forest of *Querco-Pinetum*. In the tree layer occur similar quantities of pine and oak and rarely birch. The shrub layer embraces aspen (*Populus tremula*), hazel (*Corylus avellana*), juniper (*Juniperus comunis*) and covers about 30-40% of the area. The herb layer is dense and covers about 90% of the forest bottom.

Litewniki II — the stand is situated in the complex of fresh mixed forest (*Querco-Pinetum*). The tree stand is created by the pine and admixtures of oak and spruce. Similarly as above, the canopy cover is almost full. The brushwood is constituted by oak and hornbeam shrubs and they cover only 30% of the stand area. Well developed is the herb layer, vegetation constituting it creates a carpet covering the forest bottom.

OAK-HORNBEAM FORESTS

Mierzwice I — the stand is situated in the oak-hornbeam forest belonging to the *Tilio-Carpinetum* typicum complex. In the tree layer dominating is hornbeam (*Carpinus betulus*) and pine (*Pinus silvestris*); moreover, occuring is a considerable admixture of oak (*Q. robur*), and single lime-trees and birches. The canopy covarage amounts to about 85%, also well developed is the brushwood layer (about 70%), herb layer covers, however, about a half of the stand area. In the layer of shrubs there are plants typical for oak hornbeam forests.

Litewniki I — the oak-hornbeam forest stand belonging to the T*ilio-Carpinetum* complex. In the tree layer dominating are hornbeam, pine and oak. As admixtures occur also birch and maple. Trees constitute two layers. One, as decribed above, of a height of 25 m and the second — of a height of 15 m, in which dominating is hornbeam. Coverage of the canopy is almost full (95%). The brushwood is dominated by hornbeam undergrowth and species typical for oak hornbeam forests. Well developed is the herb layer.

Thus the stands have been classified in the fertility gradient — to be expected is a productivity increasing from pine to oak-hornbeam forest, with a simultaneous increasing admixture of broadleaved trees.

MATERIALS AND METHODS

LITTER FALL

The fall of dead organic matter has been measured in monthly periods. On each stand delimited were five areas for catching of fall; those areas, each of about 2 sq. m, were covered with clear, yellow sand. After a given time, from each surface prepared in such a way collected were four samples of fall, each taken from circular areas of 0.1 sq. m. This means that from each stand collected were simultaneously 20 fall samples. The collected material was then dried for 24 hours at a temperature of 65°C. After drying, the litter was weighed and calculated was an average value for all the 20 samples as well as standard deviations.

Monthly fall series were measured during the warm season i.e. from April to November. The cleaned areas were left for the winter in order to determine the values of the winter and early spring fall collected after receding of snow.

LITTER DECOMPOSITION

Decomposition of litter has been studied with the method of "litter bags" carried out with a nylon net 0.1 mm mesh size. A large amount of mixed litter was collected on each stand in late summer and autumn. On oak- hornbeam forest stands litter was collected in October during the autumn leaf fall. The collected litter was dried first at an room temperature and then for 24 hours at a temperature of 65°C. Samples of dry litter comprising 5 or 10 g were laid out on stands at an amount of 10-30 per stand. They were distributed on an area of about 100-150 sq.m in a layer of fresh litter.

In the determined time the bags were collected and the litter was once again dried, cleaned and weighed in order to determine the mass decay. A basis for further considerations was constituted by the mean values obtained from measurements of the whole litter bag series collected at one time. The basic indices was the annual litter loss calculated in % of preliminary mass and rate of decomposition expressed in miligrames per gram per day or percent per day.

Studies in Mierzwice and Litewniki have been commenced in autumn 1986 and continued until the end of 1988. In that period collected were monthly fall samples (apart from the winter season). Studies on decomposition comprised, apart from standard measurements of annual loss of litter, also longer periods (two-year decomposition) and a few-month periods; all this was aimed at getting acquainted with successive phases of the decomposition process and dynamics of organic fall.

A special series was established for measuring one-year and two-year decomposition. In October 1986 on all stands laid out were litter bags (30 on each stand). Half of them were collected after a year in order to measure annual decomposition,

and the remaining were left in stands for the next year. The collected bags were then replaced with new ones. All have then been collected in October 1988.

In June 1987 a decision was taken of carrying out still another field experiment. On each stand laid out were at each time 50 litter bags. Those samples were then collected, 10 pcs. at a time, in the following way: after two months of decomposition (August), after four months (October 1987), after ten months (April 1988), twelve (June 1988) and at last after fourteen months from the moment of laying them (August 1988).

METEOROLOGICAL CONDITIONS IN THE STUDIED PERIOD

In the first year of litter incubation (October 1986-October 1987) noted were cool autumns and very low winter temperatures of 1986/1987 (Fig. 4).

The year was also characterized by a low precipitation (449.7 mm). The warmest month was July (17.3°C). The next season begins with draught in October 1987 and a rainfall noted in the next two months was also not high. The winter season was a period of low precipitation and relatively high temperatures. Spring rainfall was lower than a year before. On the other hand, summer was humid and very warm. Very humid months were June (190 mm) and August (100 mm). In July, a rainfall was lower.

RESULTS

ORGANIC FALL

ANNUAL FALL VALUES AND ITS COMPOSITION

On the basis of monthly measurements annual amounts of organic fall were calculated. They varied and for determined forest types were as follows:

pine forests	2.85 $t \cdot ha^{-1} \cdot year^{-1}$
mixed forests	2.98 $t \cdot ha^{-1} \cdot year^{-1}$
oak-hornbeam forest	4.59 $t \cdot ha^{-1} \cdot year^{-1}$

The lowest annual litter fall has been registered in the *Cladonio-Pinetum* forest (Table 1), and the highest values were noted in the association of *Tilio-Carpinetum* (5.06 $t.ha^{-1} \cdot year^{-1}$).

The biggest annual variations took place in the oak-hornbeam forest in Mierzwice were in the second year there was over 1 $t \cdot ha^{-1}$ less litterfall than in the first year, i.e. the difference amounted to over 20%. It is also worth noting that in the case of coniferous stands (pine forests and mixed forests) higher litterfall values were noted in the forests of Mierzwice. On both oak-hornbeam forest stands litterfall was similar (Fig. 5).

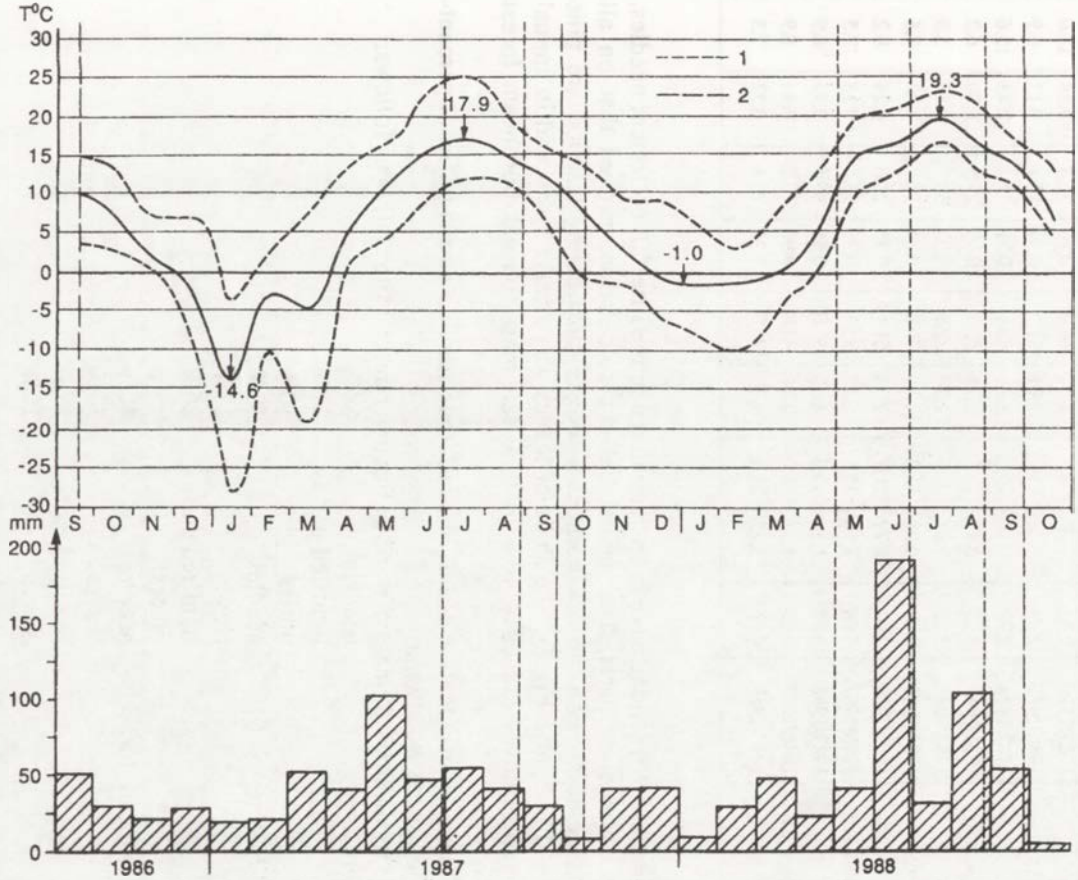

Fig.4. Monthly mean temperatures (maxima, minima, and means) and monthly sums of precipitation in Biała Podlaska meteorological station. Vertical lines mark the terms of exposition and collection of litterbags: 1-one year series, 2- two years series.

Table 1. Annual litterfall in Mierzwice and Litewniki forests

Forets type and year		Total ($t \cdot ha^{-1} y^{-1}$)	Share of litter fractions (mass and percent)							
			leaves	%	need-les	%	woody parts	%	others	%
Pine M2	1986/1987	3.52	-	-	2.55	72.4	0.66	18.5	0.31	8.8
	1987/1988	2.61	-	-	1.57	60.2	0.70	26.8	0.34	13.0
Pine L3	1986/1987	2.48	-	-	2.01	81.0	0.30	12.1	0.17	6.9
	1987/1988	2.79	-	-	1.65	59.1	0.71	25.4	0.43	15.6
Mixed-pine M3	1986/1987	3.27	0.41	12.5	1.76	53.8	0.90	27.5	0.20	6.2
	1987/1988	3.29	0.84	25.6	1.24	37.8	1.02	30.7	0.19	5.9
Mixed-pine L2	1986/1987	2.67	0.08	3.0	1.89	70.8	0.50	18.7	0.20	7.5
	1987/1988	2.62	0.29	11.1	1.34	51.1	0.75	28.6	0.24	9.2
Hornbeam M1	1986/1987	5.06	1.70	33.6	2.28	45.1	0.70	13.8	0.38	7.5
	1987/1988	3.94	1.60	40.6	1.38	35.0	0.65	16.5	0.31	8.9
Hornbeam L1	1986/1987	4.93	1.38	28.0	2.21	44.8	0.90	18.3	0.44	8.9
	1987/1988	4.41	1.25	28.4	1.63	36.9	1.21	27.4	0.32	7.3

Three basic fractions have been determined in the litterfall collected: needles, leaves and woody parts. The annual balance calculations proved that on all stands, including also the oak-hornbeam forests, dominating fraction are pine needles (Fig.5, also Fig.6). The share of leaves was always lower and in annual mean values never exceeded 40% of total fall mass (on oak-hornbeam forest stands).

A characteristic feature of fall in coniferous stands was a significant percentage of lignified woody parts.

The mean share of mass of various fractions in total litterfall is as follows:

Pine forests:	needles	68%
	lignified parts	21%
	others	10%
Mixed forests:	needles	53%
	leaves	13%
	lignified parts	26%
	others	8%
Oak-hornbeam forests:	needles	40%
	leaves	33%
	lignified parts	17%
	others	10%

SEASONAL CHANGES OF ORGANIC FALL

On all stands similar seasonal variations of the amount of organic fall are observed (Fig.7). The lowest values are connected with the winter season, and the

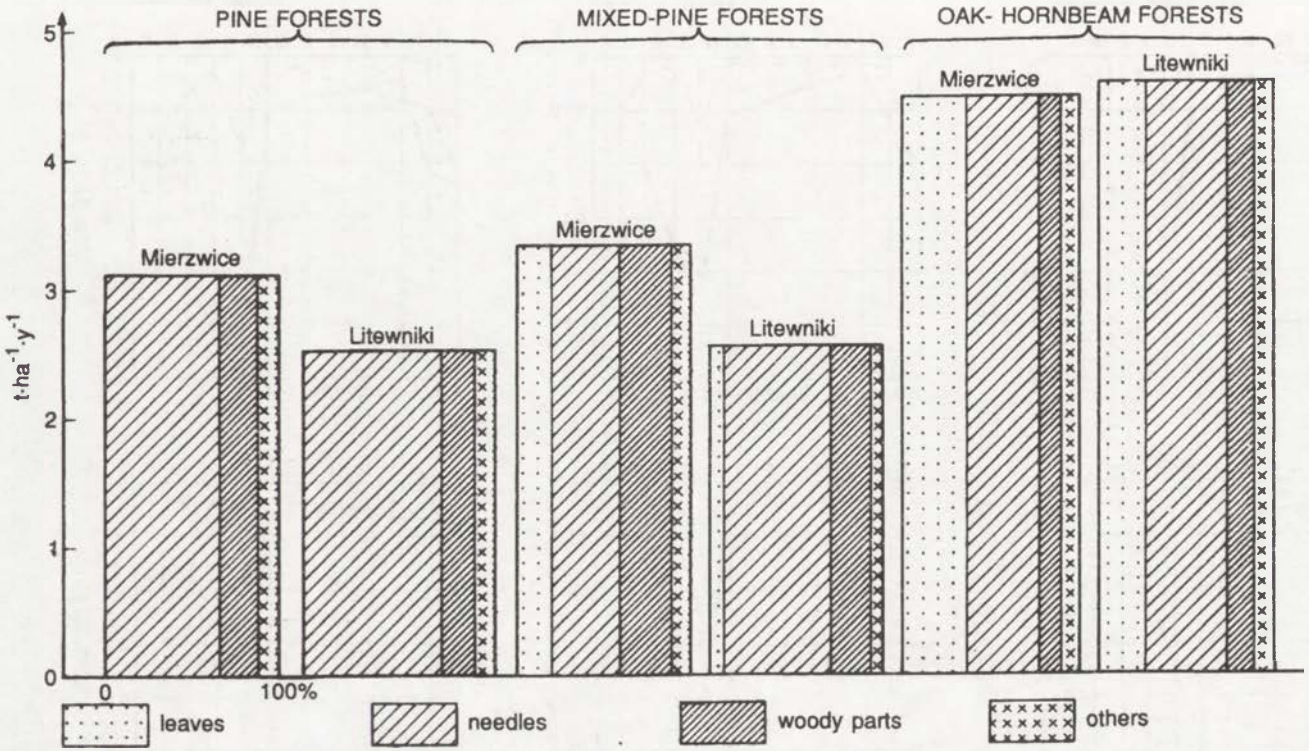

Fig.5. Mean annual litterfall and its fractions in 6 forest stands in Eastern Poland

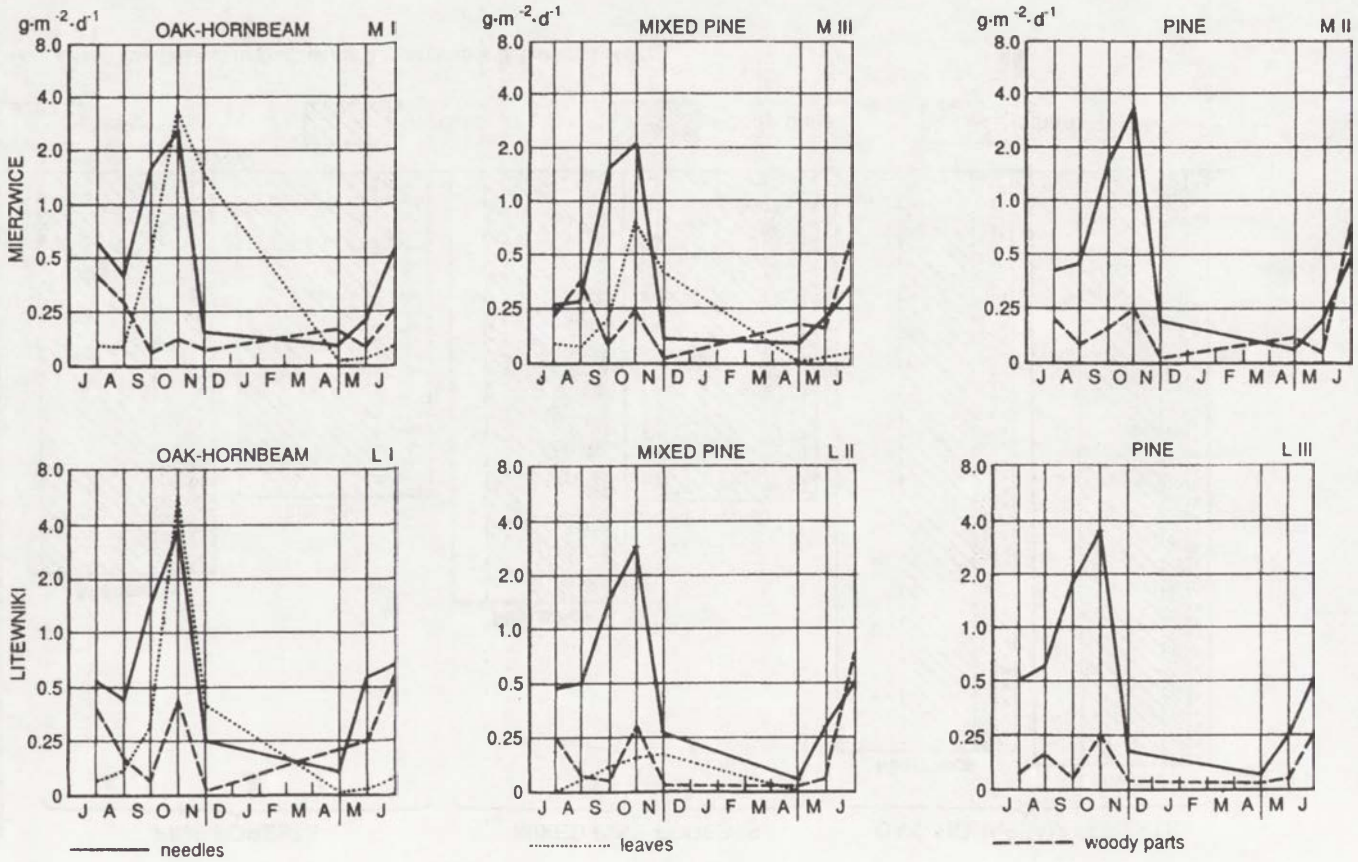

Fig.6. Seasonal dynamics of litterfall in 6 forest stands

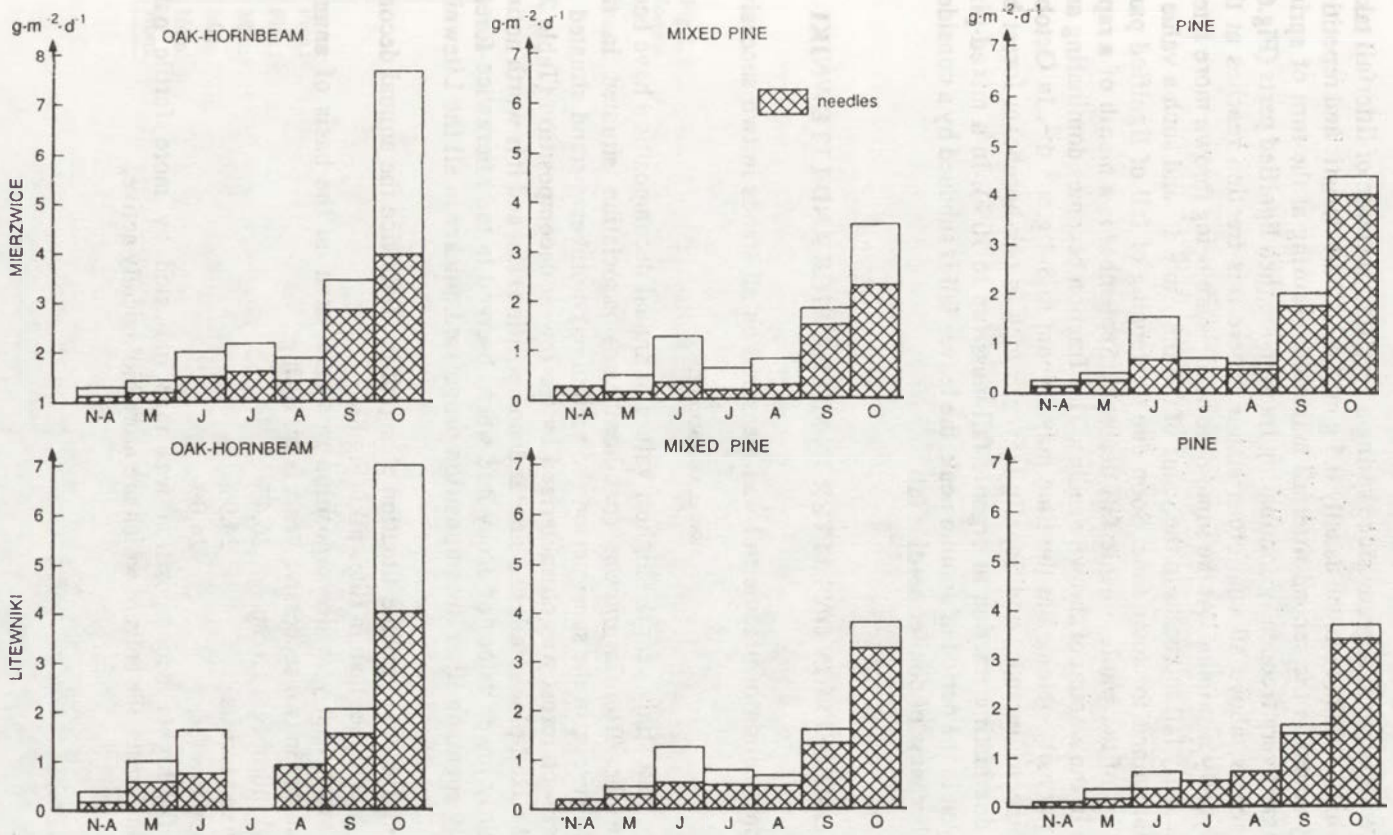

Fig.7. Share of the needles in mean monthly litterfall mass in 6 forest stands

highest with autumn. Already since spring a very slow increase of litterfall takes place, which does not exceed usually 0.5 $g.m^{-2} d^{-1}$. Characteristic and repetitive on many stands is the second litterfall maximum occuring at the turn of spring and summer; very frequently dominating fraction are then lignified parts (Fig.6). This concerns, above all coniferous stands, where this fraction reaches at the time its yearly maximum. At the same time needles are being thrown more intensely. The daily fall increases to the value of 0.6-0.8 $g.m^{-2} d^{-1}$ and such a value is being maintained for some time. Soon due to stopping of fall of lignified parts also values of the whole organic fall decrease. September is a month of a rapid increase in the amount of thrown needles. This fraction becomes dominating and the fall intensity obtained at the time may amount to 3-4 $g.m^{-2} d^{-2}$. In October the fall spectre includes additionally leaves, which in oak-hornbeam forest become a dominating fraction in organic fall mass (up to 70%). In a mixed-pine forest even in the period of autumn peak, the leaves fall is subdued by a considerably higher mass of conifer needles fall.

DECOMPOSITION ON LITTER IN MIERZWICE AND LITEWNIKI

Decomposition of organic fall was measured on all stands in two succesive years.

ANNUAL DECOMPOSITION

In the first study year the highest values of annual decomposition have been noted in the *Tilio-Carpinetum* (oak-hornbeam) association situated in the Litewniki forest; in the same period the second oak-hornbeam stand situated in the Mierzwice forest was characterized by the lowest decomposition (Table 2). Pine and mixed-pine stands had similar decomposition rate, and it is worth noting that slightly lower values of decay rate were observed in the Mierzwice forest. Generally speaking litter decomposition progressed quicker in all the Litewniki forests.

During the next year the situation changed: in Mierzwice the annual decomposition was higher than in Litewniki (Fig.8).

The mean first-year decomposition rate calculated on the basis of annual measurements in two successive years is following:

oak-hornbeam forests	26.4%
mixed forests	24.9%
pine forests	24.0%

Slightly higher decomposition was thus indicated by more fertile oak-hornbeam forests, the soils of which are more biologically active.

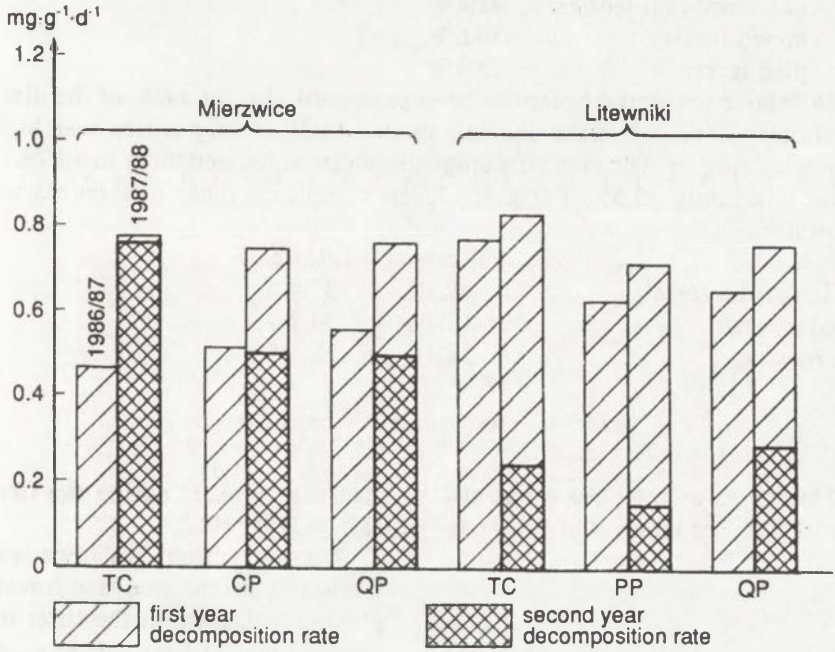

Fig.8. Decomposition rate of litter in the first and the second year of exposition in Mierzwice and Litewniki forests

TC – *Tilio Carpinetum* (oak-hornbeam forests), CP – *Cladonio Pinetum* (pine forest), PP – *Peucedano Pinetum* (pine forest), QP – *Querco Pinetum* (mixed pine forest)

Table 2. Annual decomposition of mixed litter in Mierzwice and Litewniki forests

Stand	1986/1987			1987/1988			$\bar{x}$		
	Litter decay in %	SD	Daily rate of decay in $mg \cdot g^{-1} \cdot d^{-1}$	Litter decay in %	SD	Daily rate of decay in $mg \cdot g^{-1} \cdot d^{-1}$	Litter decay in %	SD	Daily rate of decay in $mg \cdot g^{-1} \cdot d^{-1}$
Pine forest M2	19.80	1.28	0.5195	27.67	2.60	0.7397	23.74	1.94	0.6297
Pine forest L3	22.40	1.99	0.6168	26.27	2.46	0.7061	24.34	2.23	0.6625
Mixed-pine forest M3	20.13	1.89	0.5441	27.87	2.31	0.7511	24.0	2.10	0.6476
Mixed-pine forest L2	23.07	1.91	0.6337	28.33	2.06	0.7637	25.7	1.99	0.69987
Hornbeam forest M1	17.47	2.09	0.4659	29.40	2.52	0.7881	23.44	2.31	0.6270
Hornbeam forest L1	28.33	1.08	0.7657	30.41	1.86	0.8261	29.37	1.47	0.7969

TWO YEARS DECOMPOSITION

After two years differences in the litter decomposition rate between various communities became more distinct. The two-year litter mass loss was as follows:

oak-hornbeam forests	41.4%
mixed forests	36.6%
pine forests	33.4%

The above presented order has been preserved also for each of the discussed forest complexes, while the absolute rate of litter decomposition was higher in Mierzwice (Fig.9). The mean decomposition rate amounted there to 40.7%, while in Litewniki only 33.5%. For given forest complexes those differences were as follows:

	Mierzwice	Litewniki
oak-hornbeam forests	45.1%	37.4%
mixed forests	38.4%	34.7%
pine forests	38.4%	28.4%

SEASONAL CHANGEABILITY OF DECOMPOSITION

The losses of litter mass has always been the quickest during the first four months from the moment of litter bags exposition (Fig. 10).

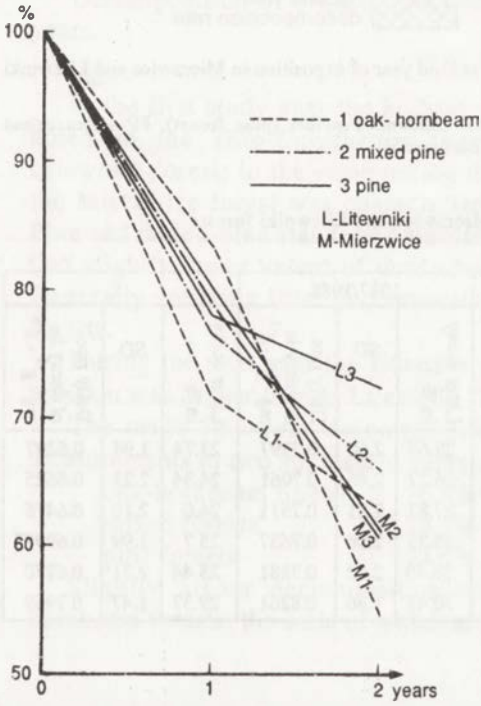

Fig.9. Two-year litter decomposition introduced as a percentage of decay of litter mass; the weight of initial samples was treated as 100%

Decomposition dynamics was different in both the analysed forest complexes. In Litewniki the litter decomposition was at first slower — during the first 64 days lost was an average of 5-6% of mass. In Mierzwice in the same period there was a loss of 12-14%. It may be assumed that during the first two months there was a loss of average about 10% of the preliminary litter mass. The next two months were a period of an intense decomposition in stands situated in Litewniki, where a further loss of 10% took place. Decomposition in Mierzwice was then clearly limited. Thanks to that, the loss observed after the fourth incubation month was similar and was in the range of 15-16%. The only exception here was constituted by the oak-hornbeam forest in Litewniki, where decomposition achieved almost 20% of the preliminary mass (Fig.10). In the further six months, i.e. from October 1987 till April 1988 the decomposition rate was slow, there was a loss of the further 3-4% of the

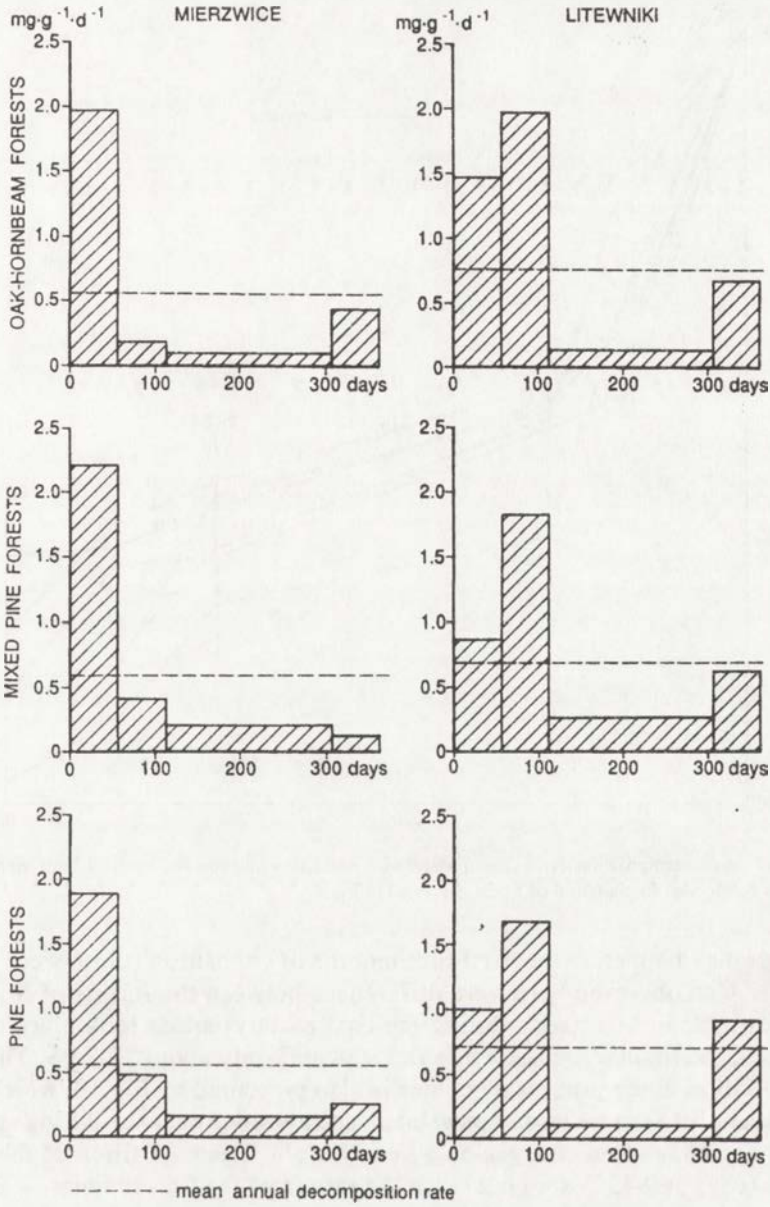

Fig.10. Differentiation of litter decomposition rates during the first 360 days of exposition

litter mass. The spring and early summer months are a period of a repeated increase of intensity in the decomposition process.

A comparison of study results of annual decomposition and two- and four-month decomposition (Fig.11.) brings to a conclusion that 60-65% of the yearly

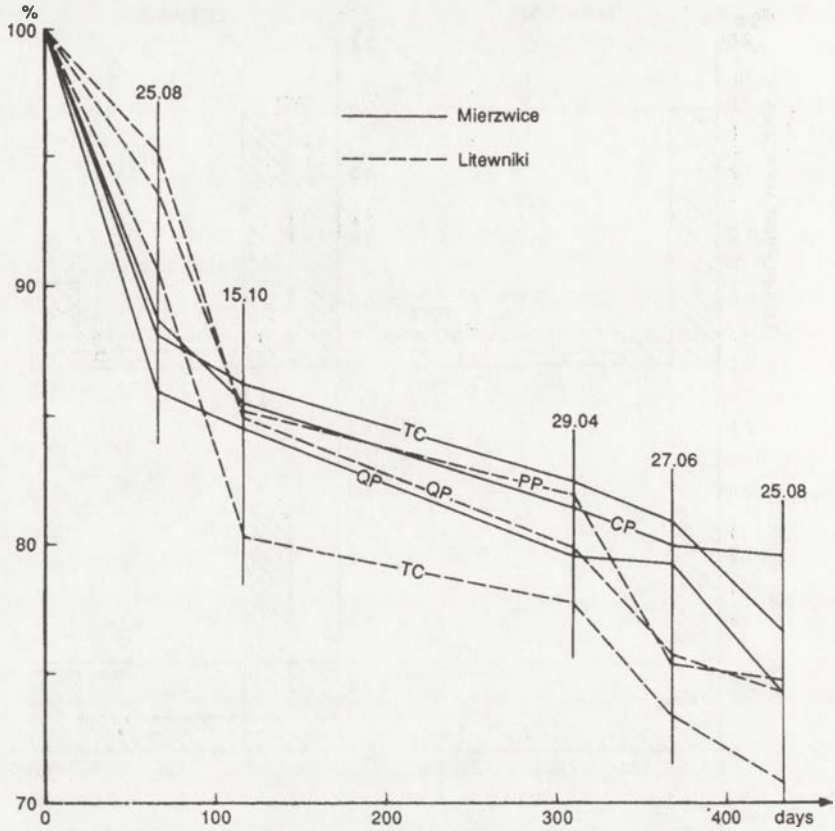

Fig.11. 430 days decomposition dynamics in Mierzwice and Litewniki forests. Vertical lines mark the dates of samples collection. Explanation of forest names as in Fig.8

litter loss may happen in the first four months of exposition (those were summer months). Also observed here were differences between the forests of Mierzwice and Litewniki. In Mierzwice during the first 60 days a loss took place of about 50% of the preliminary mass, while in Litewniki only about 20-25%. The above differentiation in the process dynamics is also presented by Fig.10, which shows also relations between the mean annual litter decomposition rate, 0.5-0.6 $mg \cdot g^{-1} \cdot d^{-1}$), and the decomposition changes on a yearly scale. Decomposition of the second summer (days 360-430) does not reach the rate from the first summer — Fig. 11.

SUMMARY

1. Organic fall in the 6 studied forests ranged from 2.8 to 4.5 tons of dry mass per hectare annually. In this mass needles constituted 40-68%, leaves 0-33%, woody parts 17-26%. Thus, despite the facts, that two of these stands were clas-

sified by a phytosociologist as oak-hornbeam forests and in accordance with an expertise of a pedologist they were characterized by a higher soil fertility from the remaining stands, the litter produced on them consisted in 40% of needles, and those needles constituted the largest fraction in the litter mass. Thus the budget of production / decomposition always includes coniferous litter with a varying admixture of leaves. Two above discussed oak hornbeam forest stands indicate another characteristic trait: organic fall contains a relatively small admixture of woody parts. This is probably due to the fact that in a forest with a smaller admixture of coniferous trees less cones are produced.

The seasonal dynamics of organic fall is similar for the needle and leafy fraction: September and October are months of a maximum organic fall in all forests. Only in some cases the second, late-spring peak of needle fall is observed.

2. Decomposition of litter is varied between stands: the mean annual loss of a litter mass = 24.0-26.4%, loss after two years of litter exposition = 33.4-41.4%. Yet always the same pattern of litter loss rate occurs: pine forests < mixed forests oak hornbeam forests, which may be explained by the increasing soil fertility and the increasing share of leaves that decompose faster. The decomposition rate is always higher— by 10-30% — in 3 forests in Mierzwice; we have no materials available which would allow us to interpret those differences occuring between forest complexes situated not so far away, in the same type of landscape.

3. An effort of carrying out a budget of production/decomposition of litter may be implemented both on whole year values, as well as through an analysis of a seasonal dynamics of both processes.

The annual mass of organic fall ranges on the studied stands from 2.8 to 4.5 tons per ha, i.e. 1.6 times; the annual decomposition range is about 1.1 (after two years of exposition 1.2) times. Thus it may be assumed that budgets of organic matter are different for various stands: everywhere almost the same, about 25% in the first year, litter loss rate is observed, while the input of litter to the forest bottom varies between stands up to 60% annually.

The seasonal dynamics of litterfall is similar in all stands: distinct peak in September-October, and, on some stands, the second small increase of fall marked in June (Figs 6, 7). The seasonal dynamics of decomposition differs in two forest complexes (Fig. 11): in Mierzwice there is one peak in first 60 days of incubation while in Litewniki the main peak occurs in the second 60 days period, it means, in the fall. The litterfall peaks last shorter, 30-60 days. The decomposition peak lasts 60-120 days; in the winter period the decomposition rate decreases evidently, and increases in the successive warm period. This second peak of the second year clearly smaller than the first one is distinct only in Litewniki. Summarizing, the seasonal peaks of litter production/decomposition overlap only partially. Much longer lasting peak of decomposition is probably conditioned by coming winter not by the shortage of material to decompose.

II. GRADIENT STUDIES OF PRODUCTION/DECOMPOSITION ALONG NORTH-SOUTH TRANSECT IN EUROPE

CLIMATIC CONDITIONS

The climate on the European continent is differentiated by crossing oceanic and continental influences (the east-west direction), as well as Arctic influence from the north and Tropic influence from the south.

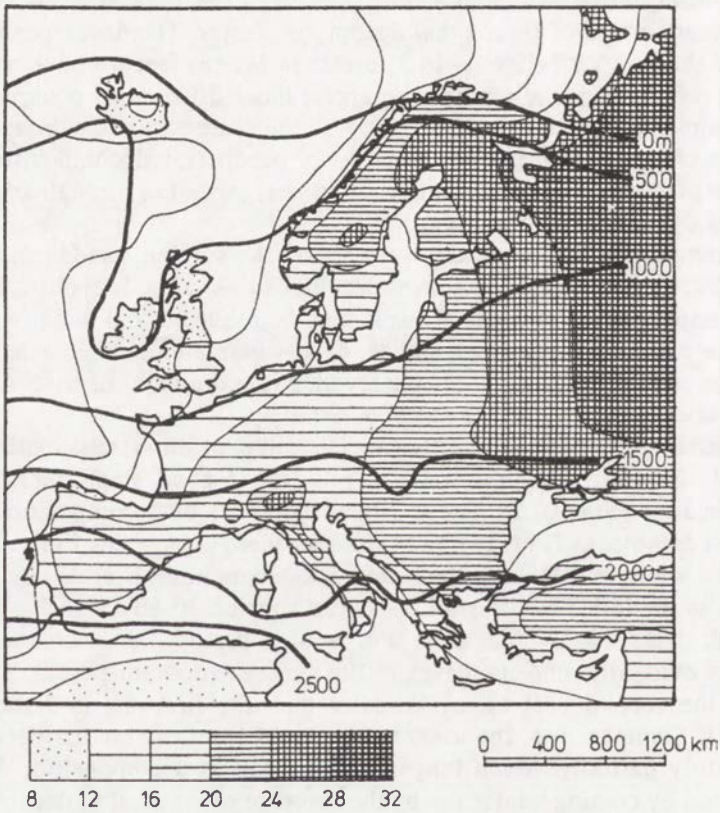

Fig.12. Climatic differentiation of Europe. Difference between the temperatures of coldest and warmest month of the year range from 8 to 32°C and are shown as darkening surfaces. Changes in the height of timber line in European mountains range from 0 to 2000 m.a.s.l. and are shown by thick isolines, (Mayer 1984, changed)

The Atlantic Ocean surrounding the European continent from the west distincly moderates temperature amplitudes in the western part of Europe — mean temperature differences between the warmest and the coldest month amount here to 8-16°C (Fig.12). On the other side, from the east, there is a significant influence of the large Asiatic continent, and differences of temperatures between the warmest and the coldest month amount to 32-36°C.

The natural change of temperatures in the north-south gradient is also considerable on the continent itself. For better orientation, let us analyse one of the measures of climate warming to the south, which is the height of the upper forest borders across the continent; as may be seen from Figure 12, the timber line in European mountains changes from 500 metres a.s.l. to 2500 metres a.s.l. This is a significant differentiation, which takes place on a small continent situated from 36°N to 71°N, i.e. on an area of 35° of latitude. A very simple index may be calculated for increased height of the upper forest border while moving to the south:the height difference amounts to 2000 m, distance between extreme points — 35°, and so, while shifting to the south by one degree of latitude the forest border in European mountains increases by 57 metres a.s.l.

On the basis of those two main tendencies shaping the climate of Europe, ascer-

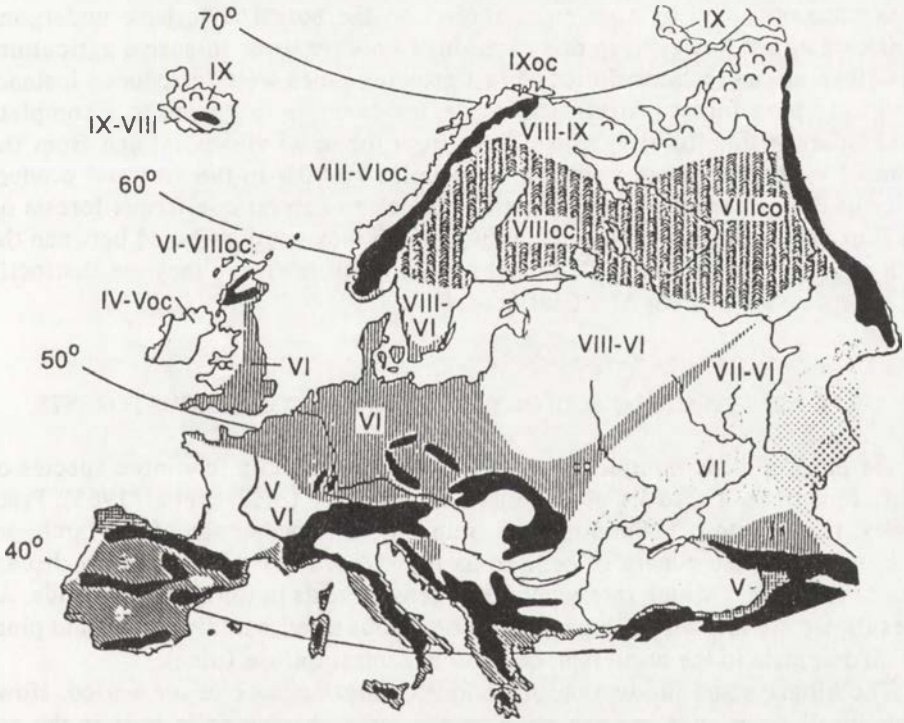

Fig.13. Eco-climatic map of Europe. Coniferous forest occurs in arctic (IX), boreal (VIII) and temperate (VI) zones, (Mayer 1984, modified).

tained and described by numerous authors, Mayer (1984) proposes the creation of an ecoclimatic map — Figure 13. On this map were marked ecoclimatic zones, in which coniferous forests occur: those are Arctic, boreal and temperate zone. In the Arctic zone, or rather in its southern belt, there is a spruce taiga, in the boreal zone all the main species of coniferous forests occur, and in the zone of temperate climate there are mixed deciduous-coniferous forests or coniferous cultures, mainly of pine and spruce, which have been introduced in Europe for many years on areas not utilized for agricultural purposes.

A similar picture is presented by W. Matuszkiewicz (1990) in his map of natural vegetation of Europe (Fig. 14). This is a new map of natural vegetation, based on rich cartographic materials collected by a large team of cooperating specialists. Zonal distribution of coniferous forest is very distinct. They are situated in east-west belts with a pattern influenced by the Atlantic Ocean. Three such belts, classically considered as the core of coniferous forests of Europe are constituted by — using the terms of Matuszkiewicz — coniferous forests of the boreal zone, as well as tundra forests stretching to the north, and in the south by mixed coniferous-deciduous forests of the hemiboreal zone. More to the south there is a zone of nemoral deciduous forests of once very rich climax forest communities; presently those forests are considerably weakened,and the majority of the areas once occupied by them has been turned over for cultivation. Also many areas once occupied by coniferous forests on the boreal zone have undergone transformations; however, in this case, due to poorer soils, intensive agriculture was given up, and monocultures of fast growing pines were introduced instead. Such long term forest management leads, for example in Poland to a complete domination of pine forests, which, both from the areal viewpoint and from the point of view of biomass production, occupies 70-80% in the area and productivity of Polish forests. However, coming back to natural coniferous forests on the European continent, it may be assumed that they are distributed between the 55th and 75th parallel of latitude and on European lowlands they are distinctly dependent upon northern Arctic influences.

SELECTED ASPECTS OF ECOLOGY OF EUROPEAN CONIFEROUS FORESTS

On the European continent there are four genera and a few more species of coniferous trees. These are pine, spruce, fir and larch (Meusel et al. 1965). Practically, taking into consideration the mainly Asiatic occurence of the larch, we will consider three genera of coniferous forests. We will also eliminate discussion of fir as well, which rarely occurs in dense forests in European lowlands. As a result, we are left with two genera of coniferous trees, namely spruce and pine, which dominate in the north (spruce), and in central Europe (pine).

The biomass and production of various coniferous species are varied. However, in all types of European conifers the most characteristic trait is the accumulation of a large mass of organic matter in litter (Fig.15).

Evenso, there is rather poor litter in comparison with the litter of broadleaf

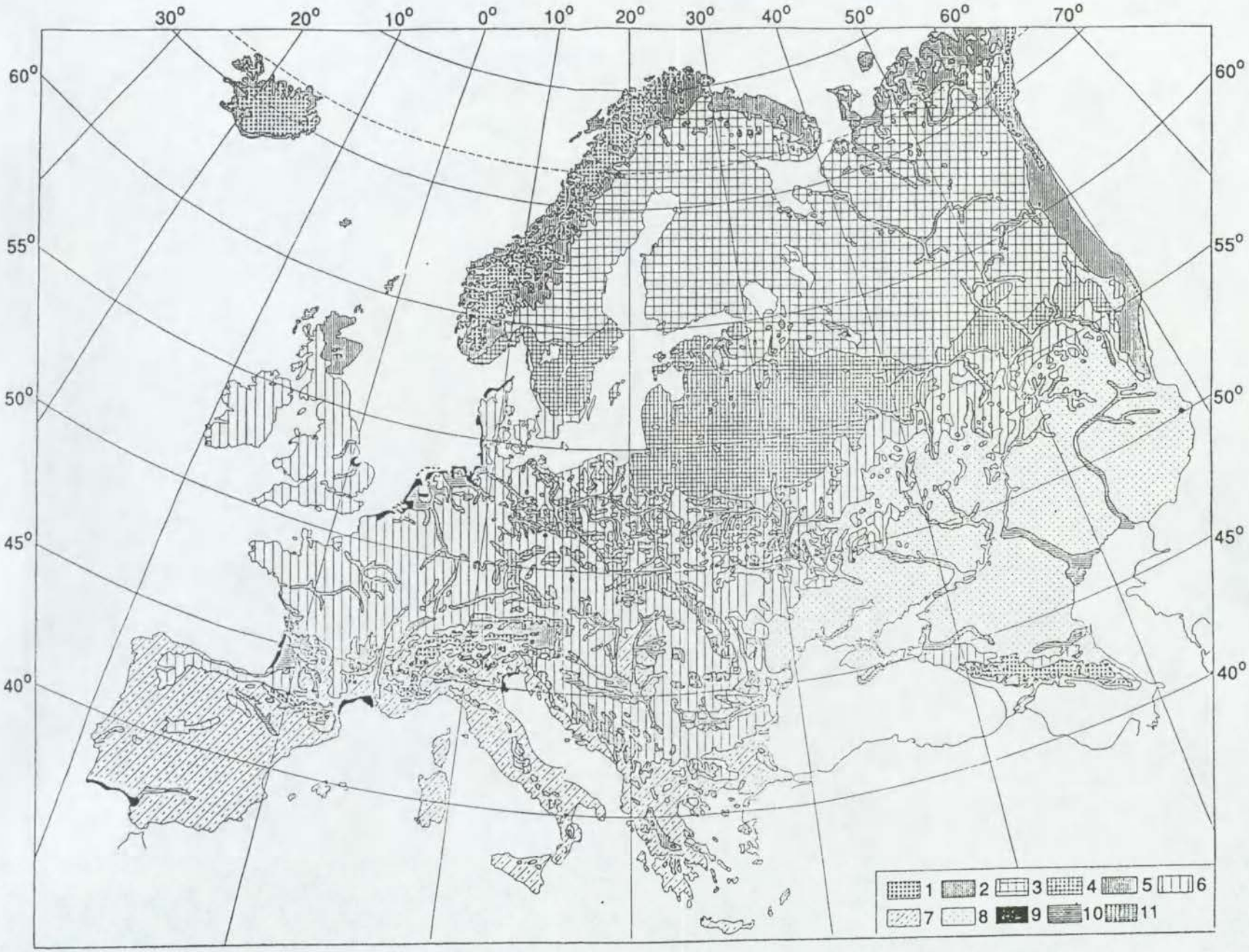

Fig. 14. Natural vegetation of Europe, after coloured map by W. Matuszkiewicz 1990 (simplified)
1 — mountain tundra; 2 — lowland tundra and forest-tundra; 3 — coniferous forests of boreal zone; 4 — coniferous and mixed forests and shrubs of hemiboreal zone; 5 — coniferous forests and shrubs of upper forest zone in European mountains; 6 — mesophilous broadleaf forests of memoral zone; 7 — termophilous forests and evergreen shrub formations of mediterranean region; 8 — forest steppes, steppes and semideserts; 9 — coastal maritime vegetation; 10 — riparian moist forests and other swampy vegetation of estuaries and the valleys of large rivers; 11 — lower forest of European mountains. Courtesy of prof. W. Matuszkiewicz

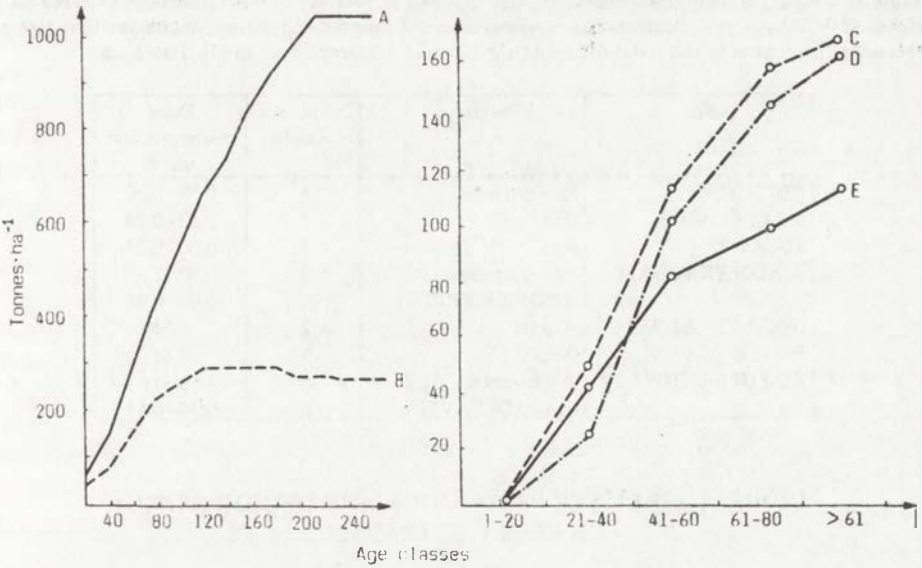

Fig.15. Aboveground litter (A) and biomass (B) accumulation in different age pine forest Pinetum myrtillosum (left, Walter 1968), and timber biomass per ha for three species of conifers in age classes: C — spruce, D — fir, E — pine, computed for the whole territory of Poland (Trampler at al. 1986; Breymeyer 1986)

forest. As coniferous forests, and pine forests in particular, are ecosystems of cool climates and poor soils, matter cycling measured by the rate of organic matter decomposition is distinctly slower here than in deciduous forests (Table 3). Interesting mechanisms for storing some essential elements in these ecosystems have been described by A. Stachurski and J. Zimka (1977). Pine trees retranslocate some essential elements from the needles before their fall. In this way the forest hold a larger portion of elements in plant tissue instead of lossing them from litter and sandy soil. Moreover, conifers shed their needles two or three times more slowly than other plants in similar climates. It seems that pine forests are systems that retain in their biomass a relatively great proportion of the elements taken from the abiotic environment. Since they are, as has been noted, ecosystems of cold climates and poor, sandy soils, their tendency to accumulate elements difficult to acquire can be seen as a positive evolutionary strategy. At present this strategy may turn against coniferous ecosystems; when the chemical composition of atmosphere and water changes rapidly due to pollution in the surrounding environment, "sparing" ecosystems which concentrate toxic substances may be subject to poisoning.

Table 3. Weight losses of autochthonous litter in forest in central Poland. Litter bags exposed on 28 stands (10-30 bags per stand) during warm season 3-4 months exposition, decomposition rate expressed as percent of initial weight. Unpublished data of A.I.Breymeyer and B.Grabińska

Site	Forest type	Number of stands	Daily decomposition rate %
BOLIMÓW	Pine and mixed	6	0.08 - 0.30
MAŁOGOSZCZ	Pine	7	0.10 - 0.24
PUŁAWY	Pine	5	0.20 - 0.24
BIAŁOŁĘKA DW.	Pine and mixed	2	0.22
	CONIFEROUS	20	0.08 - 0.30
BIAŁOŁĘKA DW.	Alder	2	0.34
BIAŁOŁĘKA DW.	Birch	1	0.44
BIAŁOŁĘKA DW	Oak hornbeam	5	0.51
	BROADLEAVED	8	0.34 - 0.51

CONIFEROUS LITTER PRODUCTION AND DECOMPOSITION ON CLIMATIC TRANSECT

Studies were conducted on production and decomposition of organic matter on a north-south transect consisting of four stands of pine forests distributed from northern Sweden to central Poland.

The rate of decomposition was evaluated by the litter bag method. The organic fall was treated as a production index (assuming that everything that falls onto the ground in the forest must have previously been produced in that stand). It was assumed that the main climatic factor influencing both ecological processes is the regularly changing temperature.

Efforts were undertaken to choose the stands in such a way that latitudinal deviations were avoided: in the central part of Europe the shifting of transect stands to the east or west would mean changing the effect of continentalism.

Studies were carried out in the years 1986-88; the main climatic characteristics of all stands are presented in Table 4. The most northern stand, Tornetrask, is outside of the aknowledged ranges of pine forests; it is in the basin of the large Tornetrask lake, ca. 200 km north of the Polar Circle, at the height of about 300 metres a.s.l. Mean long-term temperatures on this area range from -1.0 to -0,5°C (on the Tornetrask climatic post -0,7°C), rainfall ranges from 300 to 1000 mm annually (on the Tornetrask 470 mm). In the year 1986 in Tornetrask registered were -1.1°C and 476 mm. The studied stand is situated several hundred metres from the edge of a lake, often fog and ground-frosts occur on this area.

Soils were created here from poor, acid, glacial-fluvial sands originating from weathered material of siliceous rocks (Sonesson 1979). This is the border of the forest range; the undulating terrain around the lake is covered by bogs and birch tundra (*Betula pubescens* Ehrh. f. Tortuosa Led.). Among the rather homogenous low birch tundra occur stands of *Pinus silvestris* L. forest; they occur most frequently in the vicinity of the Tornetrask rail station and in the Abisko Valley.

These are thought to be relict stands of pine, as years with sufficiently warm temperatures for self-sowing of this species occur very seldom. However, our studies indicate that in stands of pine forest around Tornetrask there are numerous young and very young trees. M. Sonesson (1979) stated the same conclusion: "In the last decades increasing reproduction of the *Pinus silvestris* L. pine tree was observed". Selected for the study was one of the largest stands of pine forest (about 1000 sq. m). The age of the oldest pines is estimated at 80 years. The undergrowth plants observed were: *Betula nana*, *Empetrum hermaphroditum*, *Vaccinium victicoides* and *V. myrtylli*, *Losselueria procumbens* and *Artous alpina*. It seems that this forest is in a good condition and ought to be functioning similarly as other pine forest ecosystems. The next stand is the pine forest in Jädraås, in the central part of Sweden. The five stands from the territory of Poland studied in the transect are situated in Borecka Forest, in Mierzwice and Litewniki forests, in the Białowieża Forest (Czerlonka stand) and in two pine forests in central Poland (Kampinos and Pińczów stands).

Table 4. Main characteristics of forest on north-south transect

Stand	Geographical position		Altitude	Climate (yr)	
Tornetrask	68 °14 'N	19 °40' E	370 m.a.s.l.	-0.7°C	470 mm
Jädraås	60° 49' N	16° 30' E	185 m.a.s.l.	3.8°C	607 mm
Borecka	54 °10' N	22° 00' E	200 m.a.s.l.	6.7°C	579 mm
Czerlonka	52° 41' N	23 °40' E	175 m.a.s.l.	6.6°C	626 mm
Kampinos	52° 22' N	20 °50' E	120 m.a.s.l.	7.8°C	552 mm
MIE.II LI.III	52° 20' N	23° 00' E	165 m.a.s.l.	7.2°C	499 mm
Pińczow	50 °30' N	20 °25 'E	200 m.a.s.l.	7.6°C	595 mm

The transect extends between 68° to 50°N, and so it covers about 18°. The difference of temperatures between the most northern and the most southern stand amounts to 8.4°C. All forests studied on this transect are situated on sandy soils, in the herb layer they have shrub berries and mosses. Admixtures of the other tree species are insignificant.

Organic fall was caught on 10-20 surfaces; they were smooth circular areas, cleared of vegetation and covered by sand, each 0.1 sq. m. In such a way litter fall was gathered from the ground surface and additionally the production of the undergrowth was observed, which in case of conventionally applied litter traps located at the height of one metre is impossible. Once a year the dropped fragments of plants (seldom of animals) were collected and transported to the laboratory, fractioned, dried at a temperature of 90°C, and then weighed.

The decomposition of organic matter was evaluated by the method of litter bags. At each stand, from litter collected during the year on litter fields, portions of 10 g were prepared, placed in nylon bags (net diameter 1 mm) and placed on the same stand for the period of one year. Samples of mixed litter, i.e. composition of various fragments as they fell onto the forest floor, were exposed in such

a way; moreover,selected were various fractions of litter and were exposed similarly for decay.

Table 5. Litterfall in coniferous forests, north-south transect

Stands names, number, years of sampling	Litter fall		
	$G.m^{-2}.y^{-1}$	% needles	% woody parts
Tornetrask 1; 1986, 1987	55.3; 61.5	47.0; 63.4	48.0; 37.0
Jädraås 4; 1986, 1987	112.6; 199.1	47.5; 46.3	52.5; 53.0
Mie.II Li.III 2; 1988	224.0; 241.4	53.1; 60.0	25.7; 27.2
Kampinos[1] 2; 1975	231.7; 244.6	63.9; 54.2	26.5; 29.5
Index I: $\frac{\text{Kamp}}{\text{Torn}}$	$\frac{238.1}{58.4} = 4.08$	$\frac{58.0}{55.2} = 1.07$	$\frac{28.0}{42.5} = 0.66$
Index II[2] : Rate of change per 1°C	$\frac{179.7}{8.5} = 21.1$	$\frac{3.8}{8.5} = 0.45$	$\frac{14.5}{8.5} = 1.71$

[1] After Józefaciukowa 1975
[2] Calculated as ratio of differences between extreem litter masses and temperatures $\frac{m_n - m_1}{t_n - t}$

Table 6. Decomposition in coniferous forests, north-south transect

Stands names, numbers, sampling years	Yearly decomposition rates %				
	Mixed Litter	Needles	Branches	Cones	Birch Leaves
Tornetrask 1; 1986, 1987	11.4-14.0	14.2-15.0	4.8	2.3-3.6	3.0
Jädraås 4; 1986, 1987	17.8-19.1	27.0-29.1	5.1-6.4	7.1- 11.4	
Borecka 2; 1987	22.3-23.7	36.9	13.6	13.9	
Czerlonka 1; 1987, 1988	22.9-23.4	34.9	19.2	17.1	55.1
Pińczów 1; 1987, 1988	27.3-28.4	40.2	12.7	11.8	
Index I: $\frac{\text{Pinc}}{\text{Torn}}$	$\frac{27.8}{12.9} = 2.15$	$\frac{40.2}{14.6} = 2.75$	$\frac{12.7}{4.8} = 2.64$	$\frac{11.8}{2.9} = 4.0$	$\frac{55.1}{30.0} = 1.83$
Index II: Rate of change per 1°C	$\frac{14.9}{8.3} = 1.80$	$\frac{25.6}{8.3} = 3.08$	$\frac{7.9}{8.3} = 0.95$	$\frac{8.85}{8.3} = 1.06$	$\frac{25.1}{9.3} = 3.02$

The comparison of litterfall/decomposition rates on the whole transect, from Tornetrask to Pinczów, was presented in Tables 5 and 6. Only 55-61 g of litter falls on each square meter of circumpolar forests in Tornetrask; this litter decays slowly, 11-14% per year. In Jadraås, in central Sweden, the fall of litter is twice as large, the decay rate is also higher, although it does not change as rapidly as does organic fall. It is interesting how decomposition changes with transformations of the climate. Mixed litter (composition identical to that which falls on the bottom of the forest) has decomposition ranging from 11% in the north to 28% in the south. Pine needles decay most rapidly — from 14% in the north to 40% in the south. The biggest differences were observed in cones -if extreme values are considered-cones increase their decomposition as much as 5-fold after shifting 18° south from Tornetrask. On the average, after a shift of 18° to the south of

Tornetrask the decomposition of mixed litter and birch leaves increases twice, of needles and small twigs almost three times, and of cones — four times. The leaves of birch decay most rapidly — 30-50% per year; when the ratio of the most southern to most northern stand is compared (Pinc/Torn Index) the birch leaves stay in the low position (Index I = 1.83). But when the Index II is calculated, the most rapidly decomposing birch leaves and pine needles shift on the first position: their decay rate changes about 3% per each 1°C of temperature change.

CONCLUSIONS

1. Decay rate of woody litter fractions particulary of cones and bark is very low; for such slowly decaying parts as cones a period of about 30 years would be required for a complete decomposition.

2. The decomposition of those woody fractions reacts most distinctly to warming-colling of the climate.

3. Remembering that it is acknowledge that the decomposition of litter encompasses at least two phases: fast initial decay of carbohydrates and slow of lignin and cellulose, it can be assumed that the climate change conditions differently various decomposition phases. It stimulates stronger the slow lignin-cellulose phase.

4. Litter fall of the northern stands comprises to a much greater part lignified, slowly decaying fragments.

5. As we move to the south, the composition of litter changes, it contains more remains of soft, green parts of plants.

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SIMULATION OF THE BIOTA AND CLIMATE INTERACTIONS AND FIRST ATTEMPT AT THEIR MAPPING

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DIMITRY V. TURKOV

Abstract. The results of investigation of climate sensitivity to the land surface properties connected with vegetation cover are discussed. The CCAS climatic model has been designed in Computing Center of ASRF to study global and regional climatic shifts that emerge if the land — atmosphere properties are altered by anthropogenic or natural processes. The model was used to evaluate the sensivity of climate to prescribed variations of albedo and soil moisture. It was found that sensitivities for 1% change of the surface albedo are the following: surface air temperature -0.3°C; lower troposphere temperature 0.5°C; upper troposphere temperature -0.9°C; precipitation -0.1mm · day^{-1}

Key words: albedo, climatic model, climate sensitivity, vegetation, deforestation.

ORIGIN OF THE PROBLEM

Increasing of the interest in the evaluation of the large scale anthro-pogenic impact on climate and environment is connected with the worsening of the ecological situation in highly populated industrial regions and broadening of man made influence on nature. Yet in sixties Jay Forrester using world dynamic model showed that environment parameters changes may be very important limiting factor of the human society development.

One of the most bright example of the international efforts of investigation on global anthropogenic effects on climate and environment is the greenhouse effect of carbon dioxide. At first the task was to evaluate the reaction of the most important environmental factors like climate parameters, water resources, vegetation cover, chemical structure of the air and so on.

Now it is more clear that due to nonlinearity of the system the induced changes of the physical properties of the surface or air may significantly influence climate. Moreover, the additional anthropogenic impacts like aerosol pollution or land surface changes may have the comparable (with an increasing CO_2 concentration) consequences for climate parameters.

In this paper we discuss the results of investigation of climate sensitivity to the land surface properties connected with the changes of vegetation cover. We will not discuss the influence of vegetation on chemical structure of the atmosphere, although it plays an important role in chemical cycles, for example in

carbon cycle, but concentrate on such parameters like albedo and soil moisture responsible for energy and moisture exchange between land surface and atmosphere. Now these parameters are being changed very fast as a result of anthropogenic and natural processes like deforestation, desertification, agriculture activities and so on.

VEGETATION COVER VARIATIONS AND CLIMATE CHANGES

Vegetation covers more than 80% of the land surface. It is absent completely on glaciers (10%) and practically also on the vast areas of the pebbly, sandy, stony and salt-marshy surfaces of the most arid deserts of the Sahara and the Arabian peninsula (another 10%); although even in these deserts the vegetation survives along the dry valleys and mountain bases. The share of the land surface in the global water and heat exchange with the atmosphere is relatively small comparing with the ocean. The evaporation from the world ocean gives about $460 \cdot 10^3$ cu.km of water, from the land surface — only about $70 \cdot 10^3$ cu.km (Lvovich 1986).

Still the land surface with its vegetation cover is more important for climatic changes due to more expressed differences in the space and time. The temperature differences determined by differences of the sun radiation and heat advection are amplified by the diversity in vegetation types and seasonal growth phases. The vegetation cover on land surface is highly sensitive to the anthropogenic impacts — to deforestation, ploughing up of steppes, desertification, irrigation etc. As a result, the changes in land surface-atmosphere interrelations are no less important for the climate changes than the "greenhouse" effect. Types of the natural vegetation cover follow the natural geographical zonation. According to the ration 07 sensibile and latent heat fluxes the zones of the superfluous moisture alternate periodically with the zones of the superfluous heat (Grigorev, Budyko 1956). The "Dryness index" changes as a result of superposition of the solar radiation absorbtion growing versus the equator by the resources of precipitation oscillating along the meridians. Both factors balance (the dryness index equals 1.0) thrice — in the zones of the forrested steppes, subtropical and tropical forests. These are the zones of maxima of bioproductivity. Other zones similar to each other are the taiga and the equatorial forests with excessive moisture (dryness index about 0.4); or the temperate and subtropical steppes and shrubbed savannas (dryness index about 1.5); or the temperate and subtropical semideserts and desertificated savannas (dryness index about 2.5) with excessive heat. The higher is the dryness index, the lower is the share of the evaporation and the higher is the share of the sensible heat received by the land surface. The ratio of the sensible and the latent heat fluxes (Bowen ratio) is equal to 3-4 in tropical deserts and drops to zero or even changes the sign in the equatorial forests with a precipitation exceeding 2800 mm. The evaporation there spends all the radiation heat and sometimes cools the air changing the direction of the sen-

sible heat flow. An analogical situation can be found only near the poles with negative turbulent heat flow over the ice sheets.

From the evaluation based on field flux measurements and the water balance calculations (Krenke, Zolotokrylin 1984) it follows that the share of vegetation zones in the total land surface fluxes of the evaporation and the sensible heat does not correspond their share in the area (Table 1).

Table 1. The share of the vegetation types on the land surface and the heat and water exchange with the atmosphere

Types of vegetation	Share in the area %	Share in the evaporation %	Share in the sensible heat exchange %
Tropical and equatorial forests	14	47	-9
Subtropical and temperate forests	22	23	15
Savannas	10	7	15
Steppes	13	7	14
Tropical and subtropical deserts and semideserts	15	8	48
Subtropical and temperate deserts and semideserts	8	5	19
Tundras and forested tundras	8	4	6
Glaciers	10	-1	-8

In accordance with the idea of the G.I.Marchook concerning the energetically active zones of the oceans one can consider the equatorial forests and tropical deserts as energetically critical of the land surface. The share of the tropical and equatorial forests in the evaporation is three times more than in the land area. The same is valid for the sensible flux from deserts.

Still presently the anthropogenic changes of the land surface are so impressive that on certain areas the natural periodicity of the geographical zonation is violated. According to statistical data (Geographical Dictionary, 1988) about 13% of the land surface free from ice ($18 \cdot 10^6$ km^2) are arable (mostly ploughed) lands. About 2% ($2.5 \cdot 10^6$ km^2) are irrigated and 1.7% ($2.0 \cdot 10^6$ km^2) drained, 0.3% (about $0.4 \cdot 10^6$ km^2) are under water reservoirs. A total of about 20% are drastically changed. One has to add to this that, firstly, approximately the same area is under pastures, and, secondly, that a significant part of the forests after hewing out changes into the "secondary forests" with the predo-minance of birches and aspens in the taiga and the jagrumas in the tropics. For example in the Vologda district in the nothern Russia, the share of the deciduous trees in the forest is now greater than in Kiev district.

These changes are followed by the changes in the structure of the heat and water balances. The 13% of the land surface under unirrigated fields evaporate only 7% of total moisture evaporated from the land surface instead of 20% which were evaporated from the forests and the steppes on the same places before cutting out and ploughing. Vice versa irrigated fields evaporate about 1000 mm of

water instead of 100-200 mm in natural conditions. Covering only 2% of the surface they bring about 5% of evaporated water. The share of irrigated deserts in the global sensible heat flux decreases from 6% before the irrigation down to 1% or even negative values after it.

The difference between land-use units may be more important than the zonal differences and vice versa, the same land-use (for example ploughing) can bring the same heat and water balance in different zones. Forested steppes and steppes on Russian plain are merged now into a single zone (let us call it "plouged steppes") differing from the "pastured steppe" zones of Mongolia. The calculation of the divergence shows that the total evaporation from the mixed forests zone (now "ploughed forest zone") is lower than evaporation from the southern taiga. That violated the regularity of the goegraphical natural zones.

Thus the natural geographical and vegetational zones are changed in reality into the "Anthroponatural" geographical and vegetational zones (Krenke 1989). One has to consider the inhomogenity of real vegetational zones by the climate modeling. The evaluation of the significance of this inhomogenity may be taken from HAPEX (Hydrology-Atmospheric Pilot Experiments), including KUREX-88 and KUREX-91, accomplished in forested steppes zone of the Russian plain.

MATHEMATICAL MODELS OF CLIMATE

The main tool for investigations of climate sensitivity is now mathematical modelling.

The climate system as a physical object consists of subsystems with different characteristic times of changing.

Atmosphere is a gaseous cover of Earth. Its thermal characteristic time equals approximately 1 month, but the dynamical one — 1 week.

Ocean is separated by an upper layer with a depth approximately 250 m which exhibits seasonal changes, and deep ocean. The thermal regime of the upper ocean changes with a characteristic time from a months to ten years. The deep ocean has a characteristic time of an order of 100 years.

Glaciers, snow, sea-ice have a high albedo and play a very important role in the energetic balance of the climate system. During the ice ages the growing and decay of glaciers proceeded with the time of an order of 10^5 years. The level of the ocean changed by 100 m.

Orography of land and geography of continents are important for atmosphere and ocean circulation.

The biotic component guides the land-atmosphere interaction and plays a very important role in climate formation. The physical properties of the surface connected with the type of the soil and vegetation are important for the hydrological regime, reflection of the radiation, heat fluxes.

The most important physical absorbed solar radiation and the degree of soil surface shadowing, sensible and latent heat exchange with the atmosphere, water

content in vegetation and in soil, roughness of the surface characteristics of vegetation are (Kondratev 1990).

THE CLIMATE MODEL OF THE COMPUTING CENTER AS RF

The climatic model of Computing Center of AS RF (CCAS climate model) has been designed to study the long-term global and regional climatic shifts that emerge as the system's properties are altered by anthropogenic or natural processes (Stenchikov 1990). The climate model comprises a hydrodynamic model for the general atmospheric circulation and a thermodynamic model for the ocean surface layer. The atmospheric model is based on the two-level model in the framework of primitive equations describing atmospheric motions in the layer extending from the Earth surface, to the isobaric surface corresponding to the pressure of 200 mb and roughly approximating the stratosphere/troposphere boundary. The convective adjustment mechanism parametrizes vertical convection and the processes of cloudiness and precipitation formation. Radiative transfer is computed to a two-stream approximation, using transmission function.

The ocean model is a thermodynamic one, with no account taken of hydrodynamic flows, and has a parametrized thermic structure. Such a model can effectively measure the influence of the ocean as an energy reservoir on the evolution of the climate system.

Finite-difference approximation of the equations for the evolution of the atmosphere and the surface ocean layer is accomplished for the whole sphere on a 12° latitude 15° longitude grid. The real geography and topography of land areas are taken into account, and the Arakawa scheme is used to compute atmospheric motions. Vertically, the troposphere is broken down into two layers of equal masses.

The non-flow and kinematic conditions on free surface are utilized for the hydrodynamic equations on the underlying surface and the upper boundary of the simulation region respectively. Solar energy inputs from the atmosphere are compensated by the thermal radiation of the surface. The ocean temperature declines in accordance with its effective heat capacity, as a result of energy transfer to the atmosphere.

The model with the high spectral resolution (42 spectral intervals) is used to describe the transport of radiation in the atmosphere. This model reacts to the variation of the large amount of different absorbers in the atmosphere (Prigarin et al. 1990). For the calculation of the surface-atmosphere interaction simple boundary layer parameterization is used based on the values of the Richardson number and prescribed roughness parameter. Bucket model is used for determining the soil moisture.

CLIMATE SENSITIVITY TO THE LAND-ATMOSPHERE INTERACTION

The CCAS climate model was used to evaluate the sensitivity of climate to the prescribed variations of the boundary conditions on land, defined by variations of albedo and soil moisture. It allows assuming the amplitude of variations which can be caused by variations of the vegetation cover.

THE SENSITIVITY TO THE LAND ALBEDO

The calculations were carried out for July permanent regime. The basic mean July regime of the atmospheric circulation was calculated with fixed climatic distributions of the ocean temperature, albedo and ground wetness (Arkhipov et al. 1987; Stenchikov and Turkov 1988).

The climatic surface albedo depends on the type of vegetation and angle of the incidence of the solar radiation to the surface (Kondratev et al. 1983). For example, albedo of glaciers in the Antarctica equals to 0.9, and albedo of sea ice equals to 0.6-0.7. Ocean has a minimum albedo in tropical regions of an order of 7%. Land albedo has maximum values in grass lands and deserts, where it varies from 0.2 to 0.28. The comparison of the results of permanent July calculations with the climatic albedo and Katayama's albedo (Katayama 1972) parametrization (globally the climatic albedo is 3% greater than Katayama's) shows that most significant temperature changes occur over the Northern Hemisphere land (Fig.1). The land surface temperature decreases by 3.7°C. The globally average temperature decreases by 0,9° C. In North Africa temperature drops by 6-8°C, in Central Asia — 12°C, in Europe — 4-6°C. Air temperature over oceans in the equatorial and subtropical regions increases by 1-2°C. The largest temperature changes take place in deserts, where the changes in albedo have a maximum value. Temperature changes are observed in whole troposphere. The summer hemisphere is most sensitive to the surface albedo. The global surface air sensitivity reaches 0.3°C per 1% albedo change, but it is lower than was evaluated by Budyko. The cooling of the air over the land leads as a consequence to shifting of the convergency zone to the south and decreasing of the monsoon precipitation.

The sensitivities for 1% change of the surface albedo are the following: surface air temperature: -0.3°C; lower troposphere temperature: 0.5°C; upper troposphere temperature: -0.9°C; precipitation: -0.1 mm · day^{-1}.

THE SENSITIVITY TO THE SOIL MOISTURE

For investigating the sensitivity of climate to the evaporation from the land, the evapotranspiration parameter was changed from July climatic value obtained on the basis of the observations (Atlas 1974) to the maximum possible value equalling to 1. Globally the evapotranspiration parameter increases by

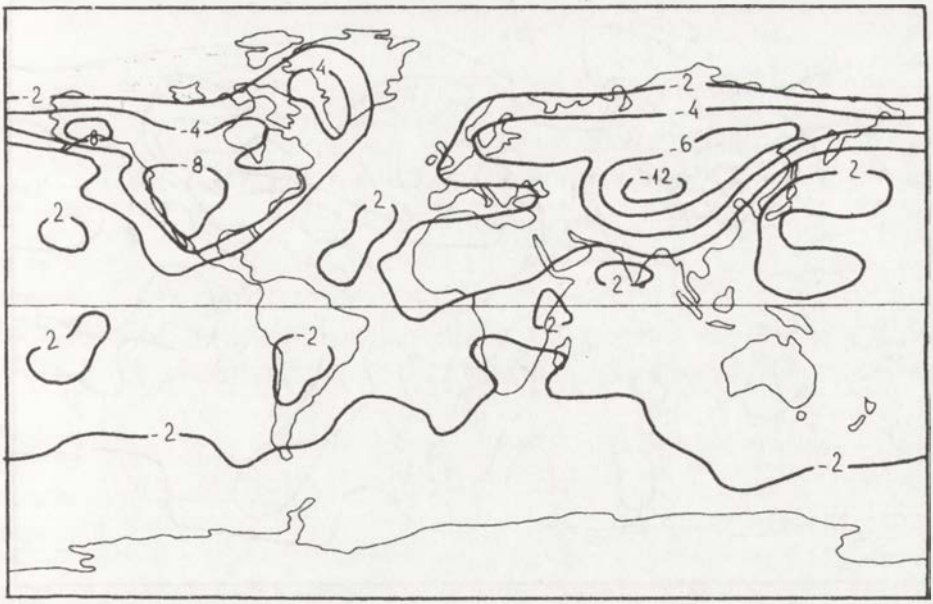

Fig.1. Air surface temperature change (°C) as a result of 3% global surface albedo increasing

0.15. The results of the calculations (Fig. 2) show that the surface air temperature decreases by 3.6°C as a result of the evaporation increase. However, changes in upper and lower troposphere are not so significant. Temperature drops are observed mainly in the Northern Hemisphere and reach 9-10°C in the latitude belt of 30-40°N , where the changes of surface wetness parameter were the largest (from 0 to 1 in deserts). The areas with a strong decrease of the surface air temperature are situated in the tropical and subtropical regions of continents. In the central regions of Europe and Asia and in North America the temperature drops by more than 17°C, and in the North Africa — more than 13°C. The increase of evaporation leads to essential increase of precipitation in many regions of Earth (globally by 0.5 mm · day^{-1}). The geographical distribution of the precipitation change shows that the maximum increase of precipitation is observed in North America and Europe and also in the northern region of the Indian Ocean and gulf of Guinea. It is obvious that changes in evaporation rate cause the most significant intensification of hydrological processes in these regions. It is very interesting that the increase of evaporation in deserts of the Northern Hemisphere, in the south-west regions of North America, North Africa and Central Asia, does not lead to a substantial increase of precipitation in these regions (Fig.3).

The sensitivities for 1% change of the surface wetness parameter are the following: surface air temperature -0.24°C; lower troposphere temperature -0.13°C; upper troposphere temperature +0.02°C; precipitation +0.03 mm · day^{-1}.

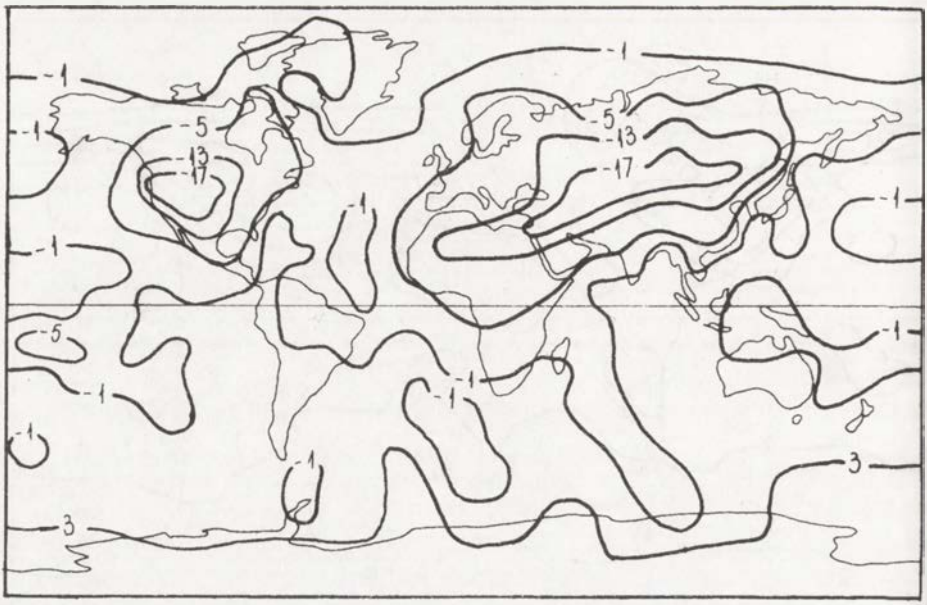

Fig.2. Air surface temperature change (°C) as a result of 15% global surface moisture increasing

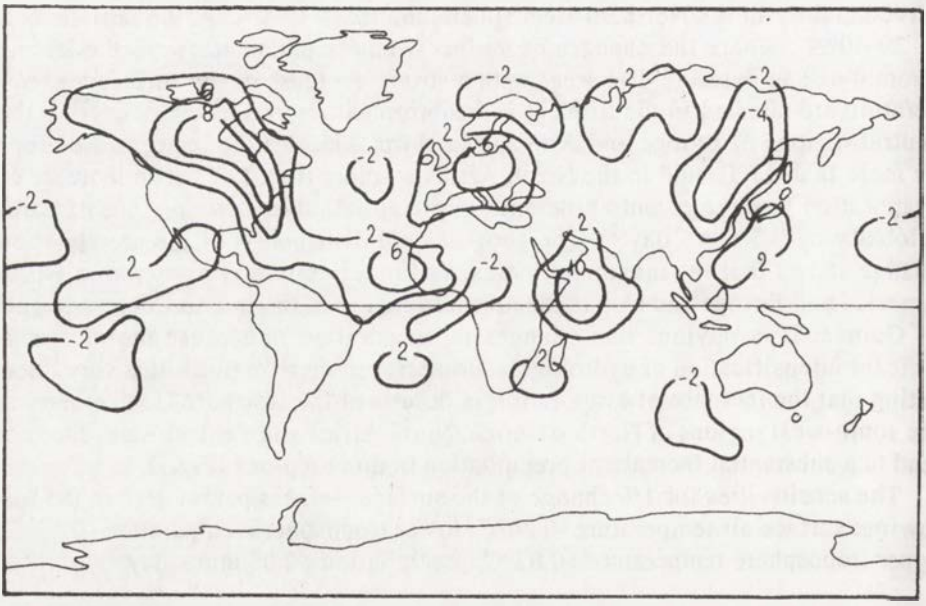

Fig.3. Precipitation (in mm · day^{-1}) changes as a result of 15% global surface moisture increasing

The effects of regional simultaneous changes of albedo and surface wetness model the regional changes of vegetation cover. The real scenarios in the case of deforestation, for example, lead to the increasing of albedo and decreasing of the evaporation. The effects of these changes on surface temperature have different signs and partly compensate each other.

The tropical forests cover approximately 14% of the land area, but give nearly 50% of evaporation fluxes from the land. The rate of deforestation in the tropics is now very high and reaches up to 10^5 sq.km^{-1} · year $^{-1}$. This leads to the decreasing of evaporation and changes in radiation balance as a result of the increasing of surface albedo.

Two numerical experiments were carried out to evaluate the climatic effect of tropical deforestation. The calculations were conducted for July and January conditions. In the regions of tropical forests in Africa, Asia and South America the albedo and coefficient of evapotranspiration were changed to the values corresponding to grasslands with substantial agricultural regions. It means that the albedo changed from a 10-14% to 18% and evapotranspiration coefficient — from 0.7 to 0.4. On average, the albedo for all regions changes by 5% and evapotranspiration coefficient — by 0.4.

The results of calculations show that deforestation has a significant influence on meteorological fields. Figures 4 and 5 demonstrate the changes of surface air temperature for July and January. The temperature in the whole tropical and partly subtropical regions increased. Changes in those regions where tropical forests have vanished are especially strong. However, the January and July reactios are significantly different. In July the changes of tropical regions are not high. In January large regions of cooling are observed in subtropical continental regions, but in the middle latitudes over Northern continents the temperature increases. This effect can be connected with the intensification of circulation due to increasing of the meridional temperature gradient and growing of energy fluxes from subtropical latitudes to the middle latitudes.

The precipitation decreases substantially not only over the regions of tropical forests but also in surrounding areas, where the surface properties did not change (Figs 6, 7). In January the precipitation decreases practically over whole South America. In July the drying covers in Africa not only the equatorial region but the Sahel, too. This shows the possibility of connections between deforestation and desertification in Africa as a result of decreasing of water vapour transport.

Experiments show that large-scale changes of the vegetation cover can cause substantial changes of atmospheric circulation and meteorological fields. The vanishing of tropical forests can lead to negative consequences not only in those regions but in a global scale. The climate changes have high enough amplitude to prevent the regrowing of tropical forests in some regions, and consequently those changes may be irreversible.

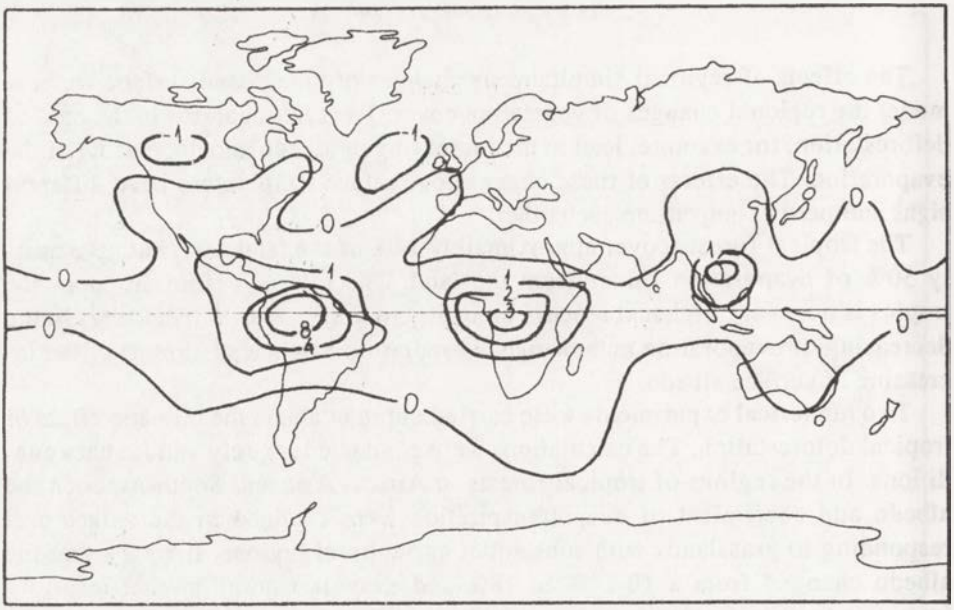

Fig.4. Changes of July surface air temperature as a result of vanishing of tropical forests

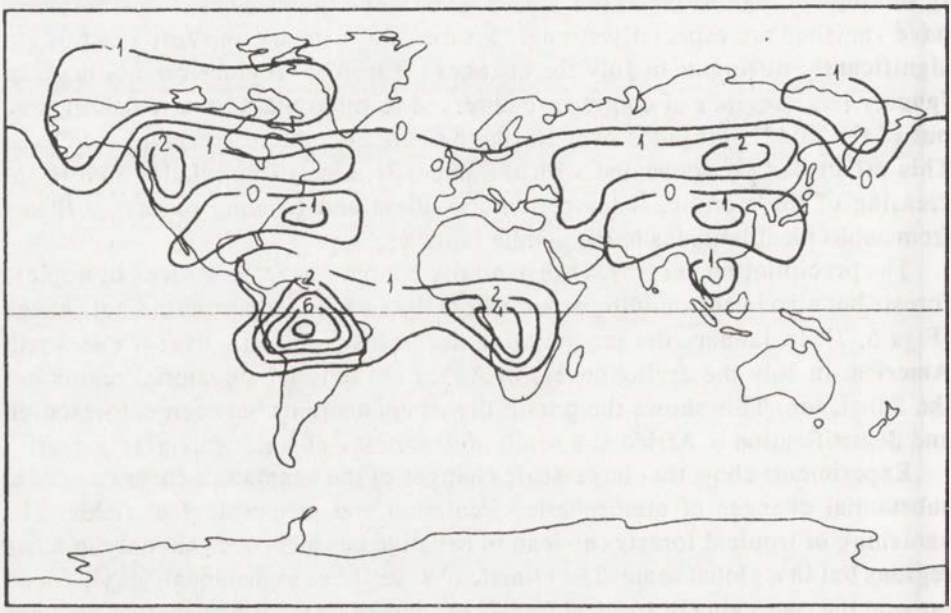

Fig.5. Changes of January surface air temperature as a result of vanishing of tropical forests

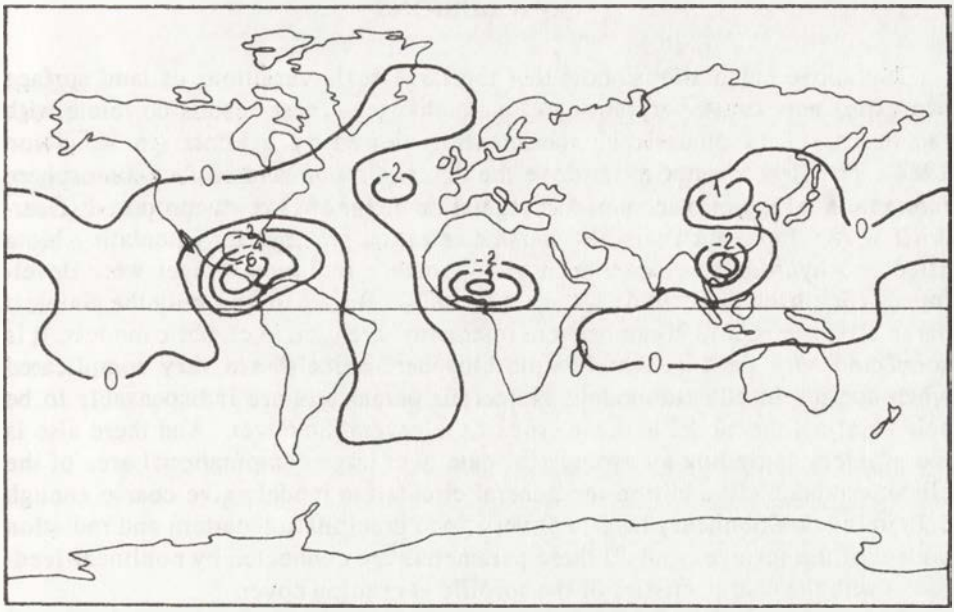

Fig.6. Changes of July precipitation (in mm · day^{-1}) as a result of vanishing of tropical forests

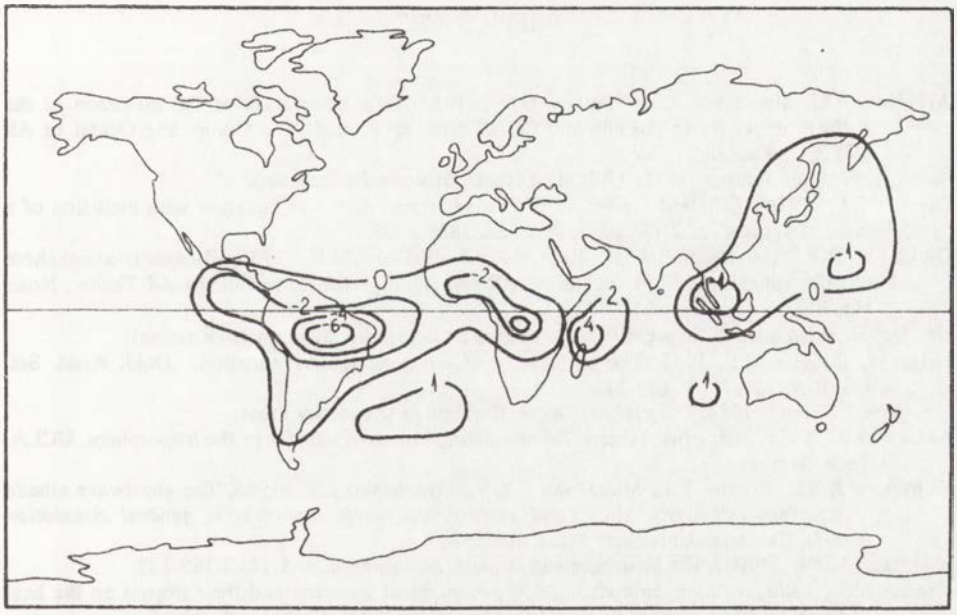

Fig.7. Changes of January precipitation (in mm · day^{-1}) as a result of vanishing of tropical forests

CONCLUSIONS

The above calculations show that the large-scale variations of land surface properties may cause very strong climate changes. These results correlate with the results of 11 numerical experiments reviewed by Y.Mintz (in Houghton 1984). The first attempt to improve the description of land surface-atmosphere interaction taking into account the vegetation cover effects was proposed (Deardorff 1978). In recent years new parameterization schemes for calculating biota effects to hydrology, evapotranspiration, surface radiation budget were develloped (Dickinson et al.1986; Sellers et al.1986). But up to now only the simplest parametrizations of land-atmosphere interaction are used in climatic models. It is connected with the fact that "simple biosphere models" are very complicated when applied in climate models. Numerous parameters are indispensable to be able to adjust the model to some type of the vegetation cover. And there also is the problem of finding an average for data over large computational area of the climatic model. In addition the general circulation models give coarse enough data in the thin boundary layer, not very good precipitation pattern and radiation budget of the surface. And all these parameters are connected by nonlinear feedbacks with the characteristics of the specific vegetation cover.

For progress in this field it is necessary, together with developing improved general circulation models and mesoscale atmospheric models, to pay considerable attention to developing simplified schemes of biota-atmosphere interaction and collect the data sets for validation of such type models.

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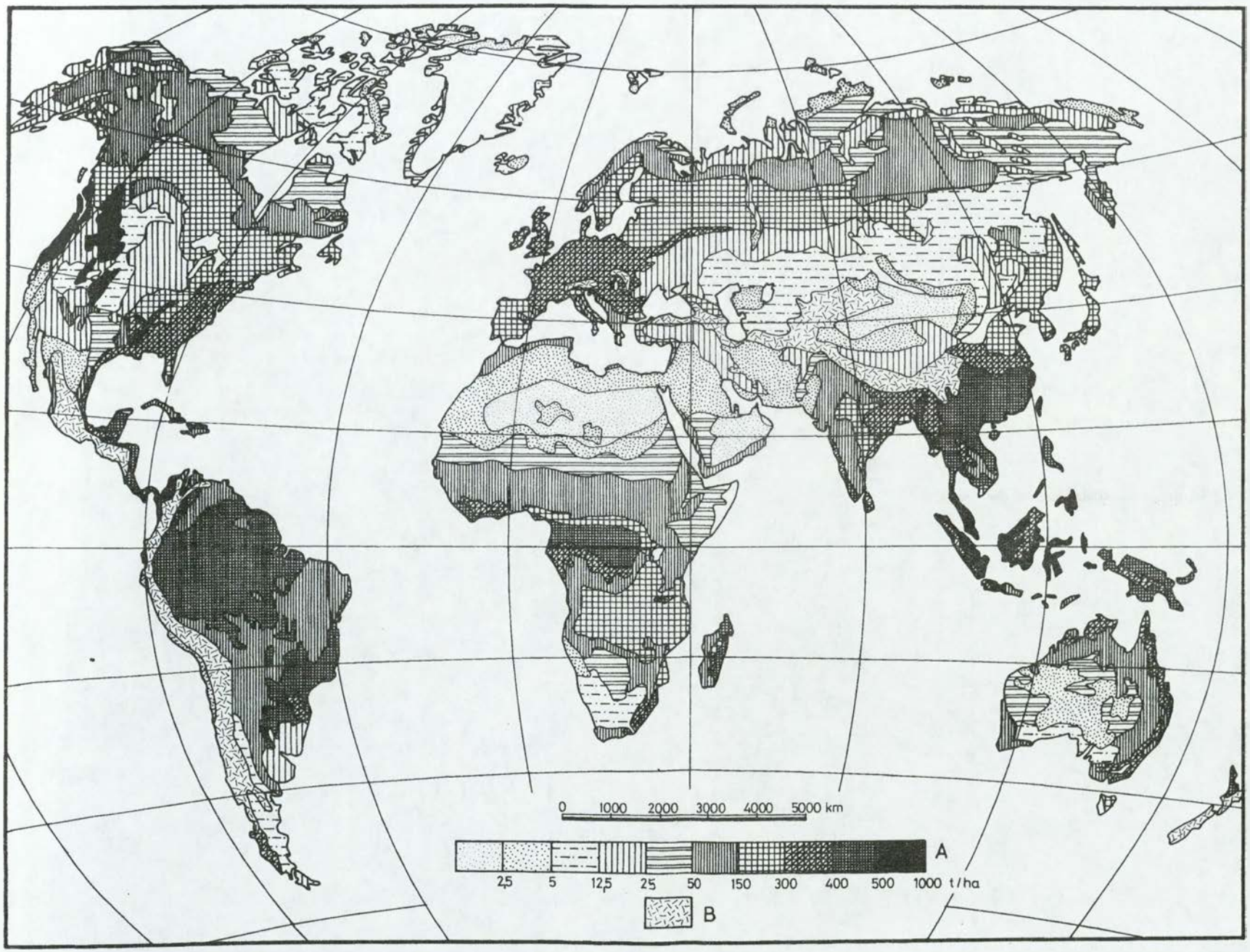

Fig. 1. Geographical pattern of global phytomass distribution

A — total store of phytomass, t per ha, B — mountain areas, with complex vegetation and significant inner spatial differencies in primary production

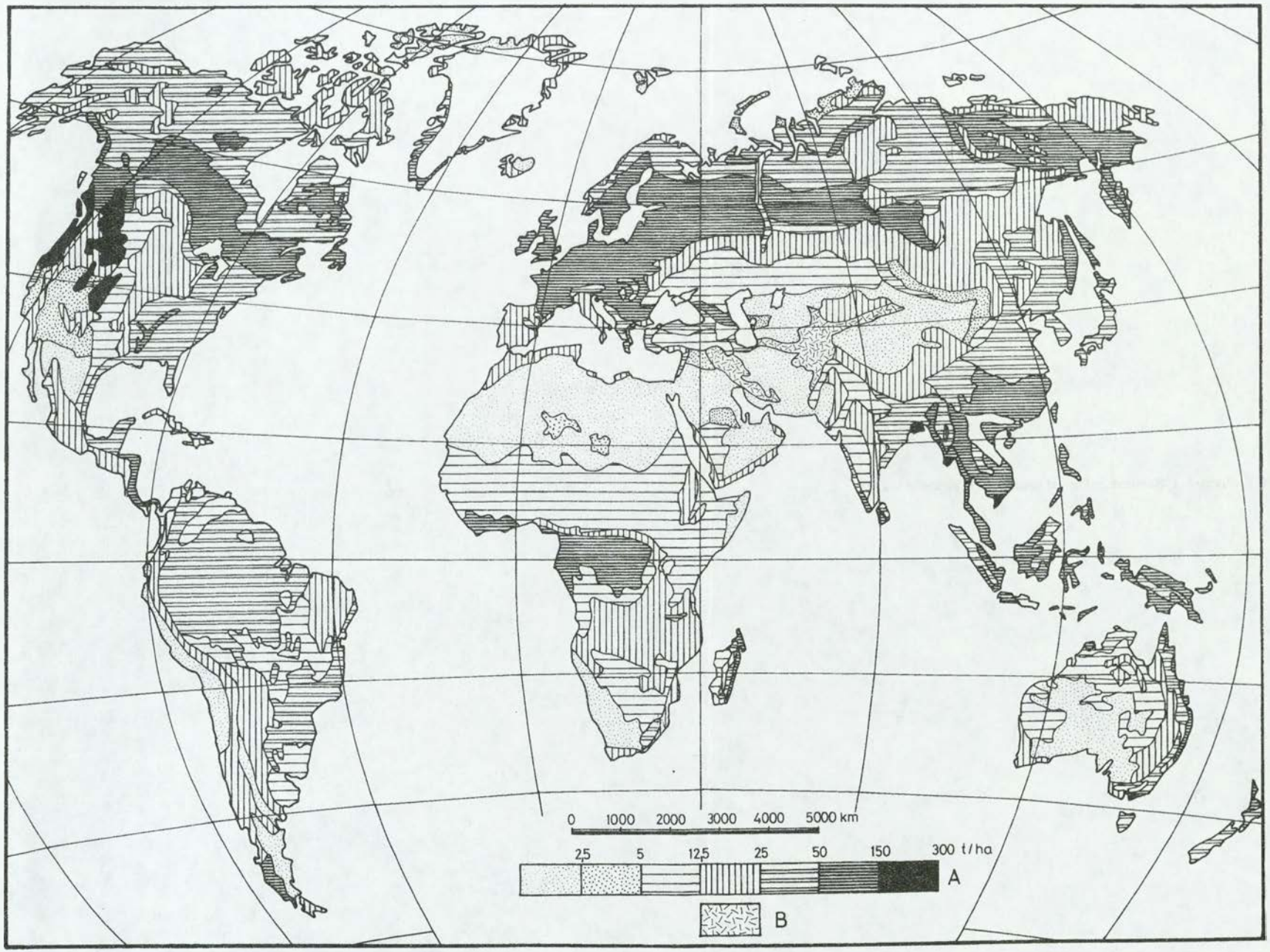

Fig. 2. Geographical pattern of global mortmass distribution
A — total store of mortmass, t per ha, B — see Fig. 1

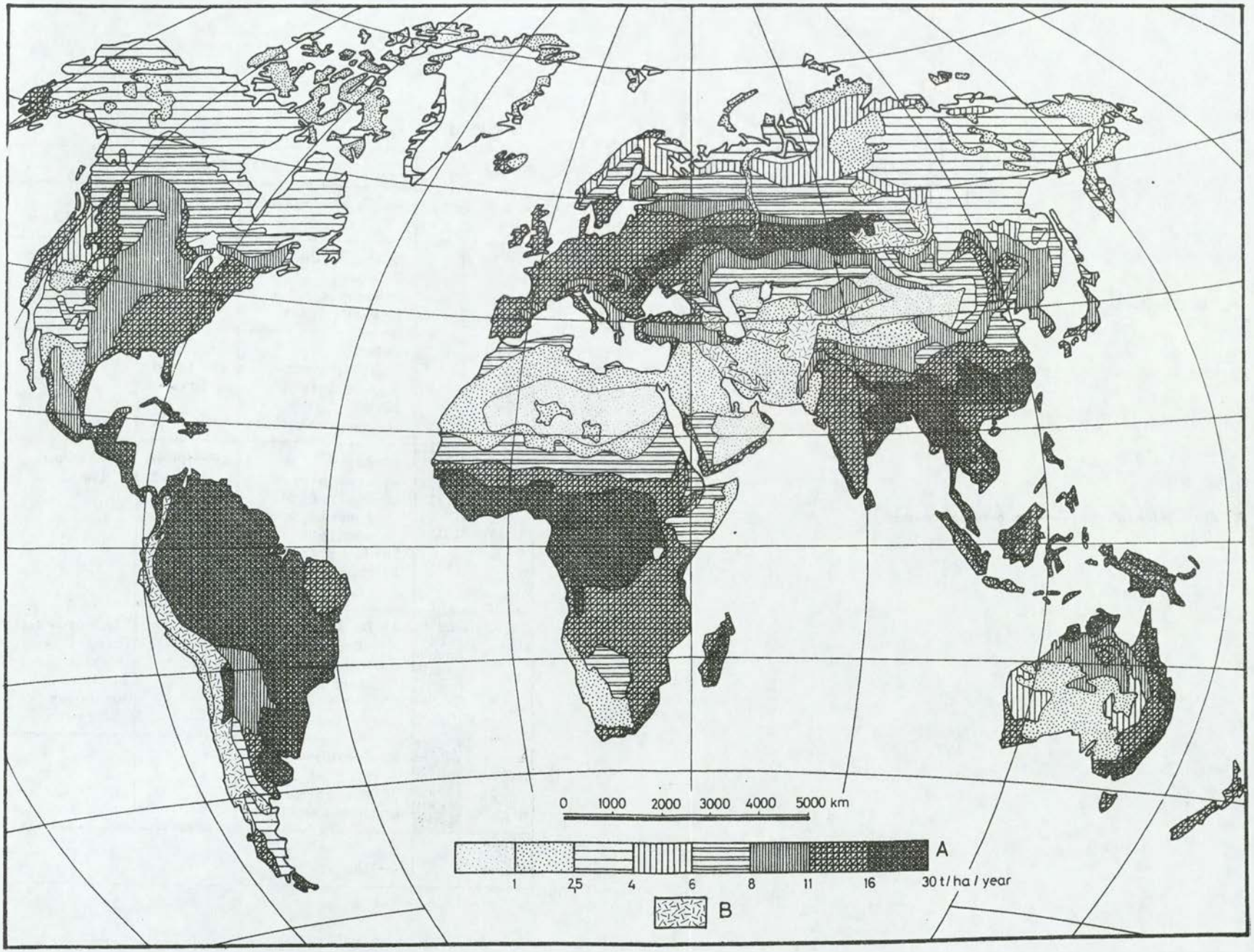

Fig. 3. Geographical pattern of global annual primary productivity
A — total primary production, t per ha per year, B — see Fig. 1

Legend to Fig. 4

Total zoomass dry weight, (kg · ha^{-1})	BIOMES		
	North Hemisphere	Tropics	South Hemisphere
Below 10 Very low	1-Arctic desert 2-Desert 5-Mount.tundra 6-Mount.desert	3-Desert	1a-Antarctic desert 4-Desert
10-80 Low	7-Tundra 8-Dry steppe, Semidesert 12-Mount.dry steppe,semidesert	9-Open woodland 10-Savanna	17-Semidesert
Middle 81-160	13-Taiga 14-True steppe 15-Subtropical forest, open woodland 18-Mount.taiga 19-Mount.meadow and steppe	16-Dense forest 20-Mount forest	17-Savanna, Pampa
161-240 High	21-Deciduous forest 23-Mount.deciduous forest		22-Deciduous forest, open woodland 24-Mount. deciduous forest
Above 240 Very high	25-Deciduous forest 26-Forest-steppe and meadow steppe		
Absent	27-Glaciers		

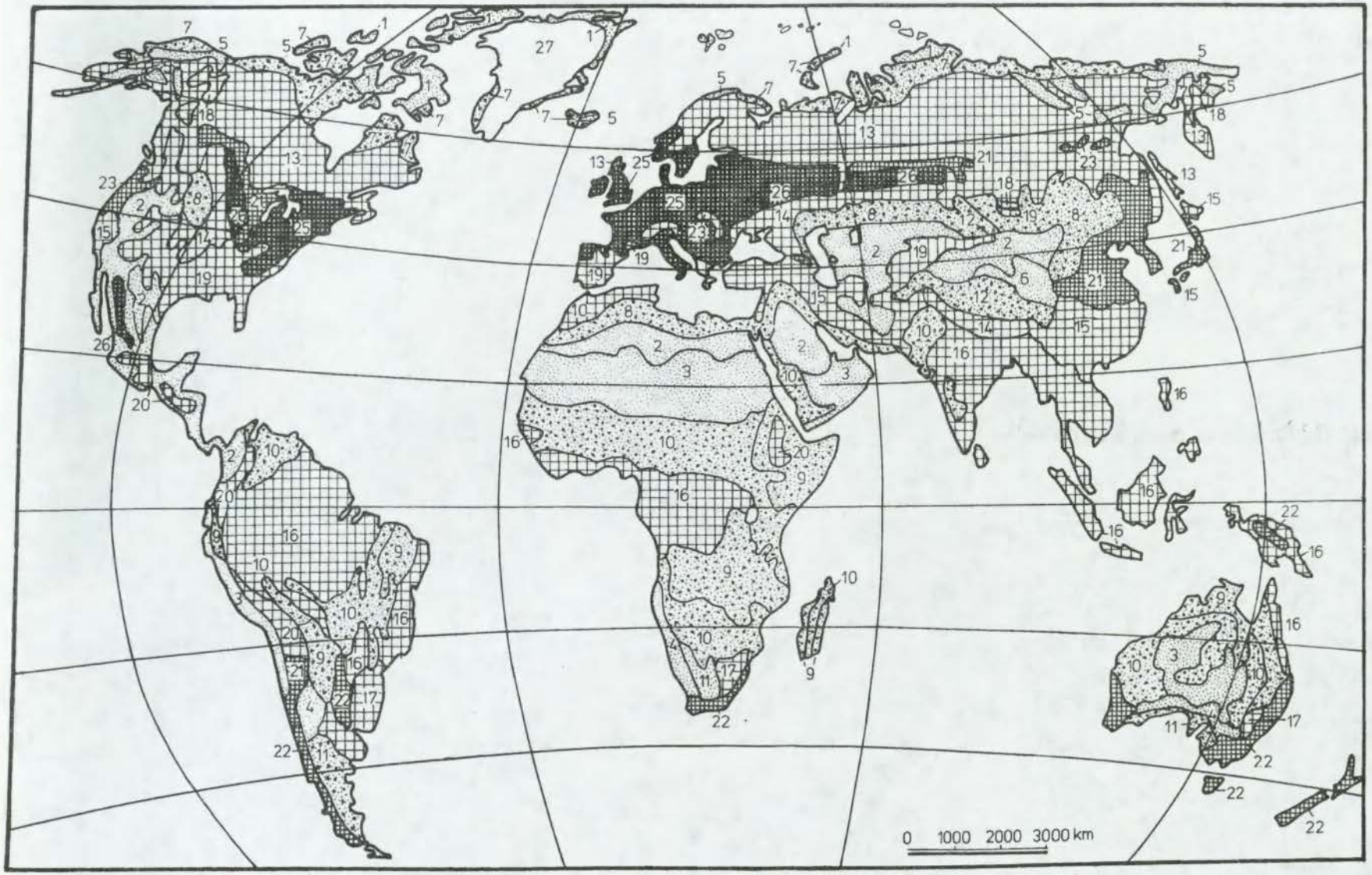

Fig. 4. Geographical pattern of global distribution of wild animals biomass (kg · ha^{-1})

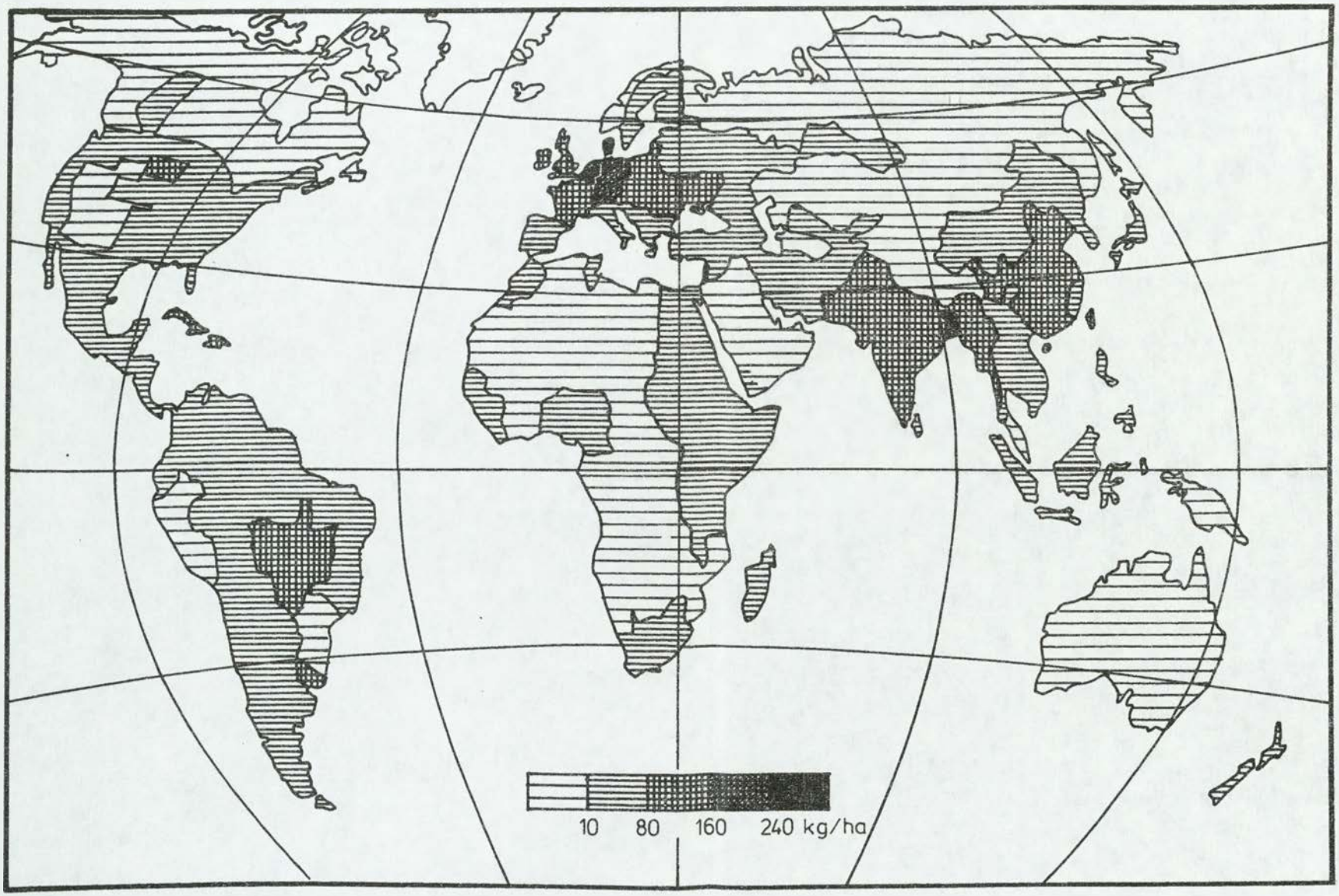

Fig. 5. Geographical pattern of global distribution of domestic animals biomass ($kg \cdot ha^{-1}$) compiled by E.V. Yasnyi and R.I. Zlotin

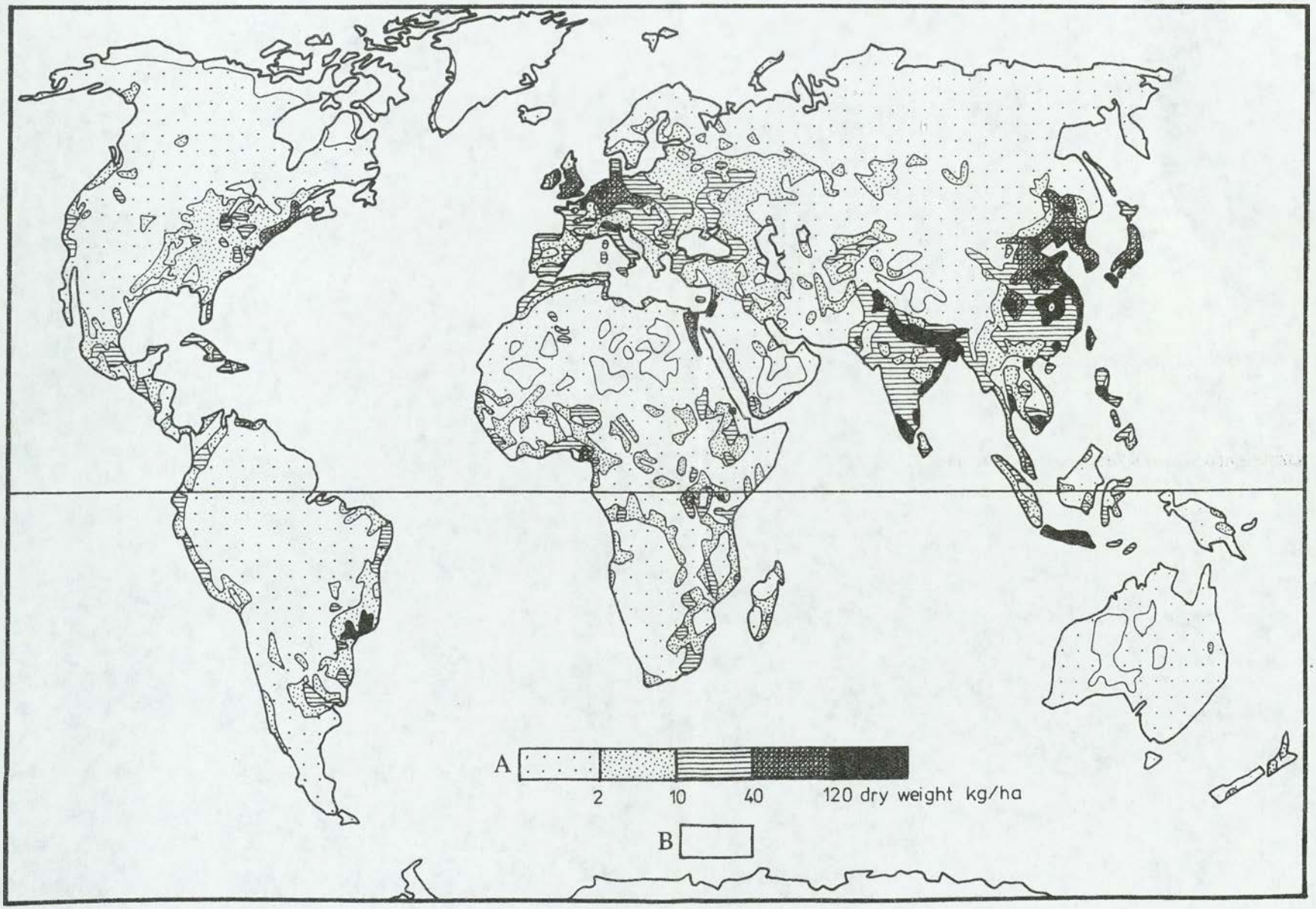

Fig. 6. Geographical pattern of global distribution of homomass (kg · ha^{-1})
A, B — see Fig. 1

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