Life cycle and population dynamics of the earthworm Lumbricus terrestris L.

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LIFE CYCLE
AND
POPULATION DYNAMICS
OF THE EARTHWORM
LUMBRICUS TERRESTRIS L.

A dissertation submitted to the
SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZURICH
for the degree of
Doctor of Natural Sciences

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FOREWORD

This doctoral dissertation was part of the research project "Simulation de la bioaccumulation et de la répartition des micropolluants dans le sol, basée sur un modèle de population de Lumbricus terrestris". The project as a whole aimed at investigating basic toxicological and ecological processes that influence the distribution of persistent organic chemicals (PCB's) and heavy metals (Cd) in and by earthworms.

The project consisted of two parts, of which one was carried out by Mr. Pierre Honsberger at the Swiss Federal Institute of Technology in Lausanne, Department of Rural Engineering and terminated in 1989 as a Ph. D. thesis ("Etude de la dynamique des PCB entre le sol et les vers de terre (espèce Lumbricus terrestris L.")").

The other part was carried out by my self at the Swiss Federal Institute of Technology in Zurich, Department of Plant Sciences and most of the results obtained are summerized in the present work. The research project was funded by the Council of the Swiss Federal Institute of Technology (grant SR Nr. 9/85-4).
Der Kreislauf der Natur


Kurt Tucholski
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1 INTRODUCTION

Soil fertility can be defined in terms of soil functions which are or are not beneficial for humanity. Several functions of the soil such as supporting plant production, decomposition of organic matter, filtering of noxious compounds from percolating water as well as its role as a habitat for many organisms are important to man. Each of these functions depends on a variety of biological, chemical and physical processes. Soil organisms influence processes at the a) chemical level: e.g. cycling of carbon and nitrogen (ammonification, nitrification, denitrification, fixation, immobilization), transformations of phosphorous, sulfur and iron (ALEXANDER, 1977), degradation of toxic organic chemicals such as pesticides, b) physical level: soil mixing, soil aeration, soil water flux, especially in macropores and c) biological level: primary production of algae and plants on the surface and below-ground, destruction of dead organic matter, predation on one or several trophic levels in the food web, parasitism, and competitive, commensalistic and mutualistic interactions between different animals, plants and microorganisms.

Communities of soil organisms consist of very different taxa with sizes ranging from few micrometers (bacteria, fungi) to several centimeters (e.g. earthworms) (see in: BURGES & RAW, 1967; WALLWORK, 1976; DUNGER, 1983). Myriads of new species remain to be described in the future. Food chains in the soil may have up to seven links, e.g. beginning with bacteria feeding on labile substrates, continuing with flagellates, amoebae, omnivorous nematodes, predatory nematodes, nematophageous mites and ending with predatory mites (COLEMAN, 1985). By comparison, food chains in epigean ecosystems are shorter, consisting of not more than four or five trophic levels, as indicated by PIMM & LAWTON (1977).

First investigations on soil biology were conducted in the last century, at about the same time when aquatic biology became a topic of scientific investigations. Pioneer studies were published by DARWIN (1881) on the role of earthworms for the building of "vegetable mould" and by MÜLLER (1878) on the importance of the soil fauna for formation of the humus forms mull and mor. A methodological advance was the development of a facility to extract microarthropods from the soil by BERLESE (1905). Nevertheless, the extraction of organisms from the soil and their systematic classification remained much more time consuming and difficult compared to those living in water. This fact, in common with the more pronounced social pressure due to waste water problems to advance in hydrobiology, may be the main reasons for the rather fragmentary quantitative studies available today in soil biology.

Methods often used to determine the role of organisms in soil processes concerned the assessment of their biomass, in few cases the estimation of their energy content or the
investigation of their respiratory metabolism. Thus, the importance of different taxa could be judged from an energetic viewpoint. According to PETERSEN & LUXTON (1982) soil microorganisms are the most important group from an energetic viewpoint, since generally they are responsible for more than 95% of the total decomposer respiration. However, total or partial exclusion of soil invertebrates from leaf litter retards the rate of breakdown and it appears that the relationship between soil fauna and microorganisms is poorly understood. Except processes such as soil mixing and soil water flux in macropores, most processes in the soil are assumed to be dependent on the compound action of microorganisms, higher plants and soil fauna (ANDERSON & INESON, 1984; ANDERSON, 1988a; COLEMAN et al., 1988).

The biomass of the soil fauna is highest in temperate deciduous forests and grasslands and decreases northwards to the arctic zone and southwards to the tropical forests and savannas, accompanied by a change in the composition of the main taxonomic groups (PETERSEN & LUXTON, 1982). Compared with protozoa, nematoda, enchytraeidae, collembola and acari earthworms may often be the greatest part of the faunal biomass in temperate deciduous forests and grasslands. Maximum biomass live weights reported were 2 t/ha in a pasture in Ireland (COTTON & CURRY, 1980), about 2-3 t/ha in sown pastures in New Zealand (SEARS & EVANS, 1953; WATERS, 1955) and 2.8 t/ha in a deciduous forest in North America (REYNOLDS, 1972). The ecology of earthworms and their role in several soil processes was comprehensively described by EDWARDS & LOFTY (1972), and LEE (1985) reviewed more recently the available literature. A short review on earthworms as components of ecosystems was published by BIERI & CUENDET (1989).

Some important soil processes generally regarded to be influenced by earthworms are: organic matter turnover; leaf litter on the soil surface is consumed by epigean earthworm species or pulled into the soil and ingested there by deep vertical burrow inhabiting earthworms. Leaf litter amounts equal to the total annual litter fall may be consumed by earthworms in a few months. Several authors cited in LEE (1985) demonstrated a rapid removal of plant litter from the soil surface by earthworms in a variety of habitats. Another source of earthworm food on the soil surface is the dung of ruminants. HOLTER (1983) found a close linear relation between the organic matter disappearing and earthworm biomass under and in pats. Dead roots and other decomposing organic matter in the soil may be the primary food source for endogeans earthworm species. Theses species are assumed to move more or less horizontally through the soil by geophagy and to be attracted by dispersed organic matter.

mineral soil turnover; many attempts have been made to estimate the quantities of soil ingested by earthworms and deposited as casts on the surface or below-ground. The most
impressive study in this domain is still the early work of DARWIN (1881), who esti-
mated in selected sites that casts corresponding to a 5 mm thick soil layer may be de-
posited on the soil surface per year. STÖCKLI (1928) estimated that about 81 t air dried
casts per ha were deposited per year on the surface of a golf-course in Switzerland. The
dry weight of yearly deposited earthworm casts as measured by several authors and
summarized by LEE (1985) ranged from 2.5 to 270 t per ha. Since several species are
predominantly subsurface-casting, the total amount per year of mineral soil passing
through earthworm guts may be considerably higher (BOUCHÈ, 1982).

mixing of organic and inorganic matter: during gut passage organic and inorganic matter
are intensely mixed. As a consequence aggregate stability (LEE, 1985) and microbial
activity (e.g. STÖCKLI, 1928; PARLE, 1963; SHAW & PAWLUK, 1986) in casts and
microbial activity in burrow walls (DÜGGELI, 1927; LOQUET et al., 1977) may be
higher than in the surrounding soil. Distinct soil horizons may disappear through the
action of earthworms in mixing organic and inorganic matter (NIELSON & HOLE, 1964;
STOCKDILL, 1982; HOOGERKAMP et al., 1983)

nutrient cycling: earthworms may contribute directly and indirectly to carbon and nu-
trient fluxes in the soil. Direct contributions are through food consumption and subse-
quent immobilization as body tissue (SATCHELL, 1963). Indirect effects of earthworms
and other invertebrates may be caused by altering the soil as an environment for mi-
crobial activities and plant roots (ANDERSON, 1988b). Earthworm contributions to nu-
trient fluxes are described for phosphorous (MANSELL et al., 1981), and nitrogen in
arable soils (CHRISTENSEN, 1987), deciduous forests (SCHEU, 1987), no-tillage
agroecosystems (PARMELEE & CROSLEY, 1988) and from organic matter applied to
agricultural soils (KNIITEL et al., subm.)

water drainage and soil aeration: earthworms construct a large macropore network sys-
tem in the soil. The volume of the macropore network changes seasonally and may range
from 1.5 to 9 l per m^2 (KRETZSCHMAR, 1982a). Macropores contribute to water in-
filtration (EHLERS, 1975; CARTER et al., 1982; AINA, 1984; SMETTEM & COLLIS-
GEORGE, 1985) and may be important to prevent superficial run off during thunder-
storms. Soil aeration may also be affected by the earthworm macropore system
(KRETZSCHMAR & MONESTIEZ, subm.)

The effects of earthworms on inorganic and organic matter turnover, soil mixing,
nutrient cycling, water drainage and soil aeration in intense agricultural production
systems in the past have been generally covered by tillage, and pesticide and fertilizer
application. As agricultural practice moves towards low inputs and sustainability as de-
sirable goals, knowledge of the activities of soil biota becomes increasingly important
(CROSSLEY et al., 1989).
The contribution of earthworms to soil processes has to be considered in relation to their biology. Their actions are supposed to aim not primarily at influencing soil processes, but at the performance of the life cycle. The dynamics of populations are due to seasonally changing environmental factors influencing life cycle traits. Benefits associated with the actions of earthworms are regarded as seasonally varying by-products of the life cycle traits performances. Life cycles of earthworms have been investigated only partially for few species, the compost inhabiting *Eisenia fetida* (Savigny) being the best known. Surprisingly, the influence of the temperature on life cycle traits of earthworms has rarely been considered. The great lack of information in this area may be attributed to difficulties in rearing species with diapause or quiescence, to a longevity of several years of some species and to the assumed low economical importance for intense agricultural production systems.

The present study was confined to the earthworm *Lumbricus terrestris* L.. This species was chosen because of its wide distribution abundance in many soils of temperate regions and the relative easy rearing. The aim of the study is to investigate the population dynamics of this species and the influence of environmental factors on life cycle characteristics. Since earthworms, especially *L. terrestris*, are key soil invertebrates in many temperate regions of the world, knowledge in this area provides the basis for a wide field of further investigations on the effects of invertebrates on soil processes at the biological, chemical and physical level.

Special care was taken in this study to give the results in a form that allows the construction of a simulation model of the population dynamics. Such a model is regarded as an important tool for further investigations in soil biology.
2 SUMMARY

This thesis consists of two parts, one dealing with life cycle traits of *Lumbricus terrestris* L. as related to environmental factors, the other with the population dynamics. Life cycle investigations included growth and maturation of juveniles, reproduction and cocoon development, and dry matter consumption and assimilation at different environmental conditions. Field studies concerned the extraction of earthworms from the soil, sampling statistics and the population dynamics of *L. terrestris*. Each of the studies is summarized separately.

The consumption rate \( C \) per g earthworm dry weight per week was described by nonlinear functions of soil temperature, soil water potential and food availability. The optimum temperature and soil water potential for food consumption are at about 22 °C and -8.7 kPa, respectively. Zero consumption occurred at -40 kPa. The maximum consumption at 15 °C was 1.05 (dandelion) and 1.23 (grass) g dry weight per g earthworm dry weight per week. A general consumption function to account for all three environmental factors is given. The assimilation rate \( A \) per g earthworm dry weight per week was defined as the sum of growth rate and maintenance rate. Maintenance could be calculated based on respiratory measurements reported in the literature, whereas growth was measured. High temperature and limiting environmental conditions, such as low food availability and low soil water potential, led to an increase in the assimilation efficiency \( \frac{A}{C} \) of *L. terrestris*. At -8.3 kPa and 15 °C *L. terrestris* assimilated 55 and 43 % of the ingested dandelion if food availability was 0.25 and 1.0 g dry weight per g earthworm dry weight per week, respectively.

The growth rate per g earthworm dry weight per week of juveniles scaled as \((\text{body dry weight})^{0.79}\). Growth rate and development rate were optimum at 23.1 and 22.5 °C, respectively. Juveniles showed the first external signs of sexual maturity (male pores, tuberculum pubertatis) 66 d and 180 d after hatching at 20 °C and 7.5 °C, respectively. The clitellum began to grow at these temperatures after 82 and 213 days, respectively. The mean dry weight of *L. terrestris* with incipient male pores was 0.47 g, that of *L. terrestris* with incipient clitellum growth 0.64 g. Mortality during the juvenile stage was 100 % at 25 °C and decreased to 0 % at 7.5 °C. Deaths occurred mostly during the change of stage.

The rate of reproduction (g cocoon dry weight per g earthworm dry weight per week) was described as a function of age by a model with two linear sections, one for the steeply increasing reproductive rates of just matured adults and another for the slowly decreasing rates with progressing age. Depending on the temperature the maximum reproduction occurred 6.2 weeks (15 °C) and 15.7 weeks (10 °C) after the onset of sexual
maturity. The longevity of the adults lasted from about 40 weeks at 15 °C and more than 56 weeks at 10 °C. At 12.5 and 15 °C an adult pair produced about 130 cocoons corresponding to a dry weight biomass of about 1.7 g during its life. Cocoons produced at the beginning of the reproductive period of an adult had a high probability of survival, whereas those from old adults mostly died. Cocoons hatched after about 61 d at 20 °C, but needed more than 350 d at temperatures below 12.5 °C. In few cases not only one, but two, three or four juveniles hatched successfully from a single cocoon.

The extraction of juveniles of *L. terrestris* was equally efficient by the simple application of formaldehyde or chloroacetophenone (teargas) solutions and by a chloroacetophenone application followed by a handsorting to a soil depth of 110 cm. For adults the combination chloroacetophenone/handsorting was more efficient than the use of chemical expellants only. The efficiency of chemical expellants for the extraction of adults could be improved through a repeated application of the chemicals at three subsequent evenings. The frequency distribution of juveniles could be described by a negative binomial, that of the adults by a Poisson distribution. These statistical distributions were used to calculate the sample size with a specified reliability. It is concluded that if adult and juvenile *L. terrestris* are abundant, their densities are reliably estimated in a homogeneous environment by taking 10 sampling units of 50 cm x 50 cm per sample.

The population dynamics of the earthworm *L. terrestris* was studied from April 1987 to September 1988 in a meadow which was frequently mowed. After mowing, the cut plant material was left on the plot as food for the earthworms, except for small samples which were removed to estimate the dry weight of the cutting per unit area. In both years precipitation occurred regularly and the soil was never dry in lower layers. Therefore, soil water was assumed to be a non-limiting factor for *L. terrestris* in this experiment. The demand for food of *L. terrestris* was calculated by means of a nonlinear function of soil temperatures given in this thesis. It was demonstrated that at the prevailing temperatures the earthworms demand for food could not be satisfied by the remaining cut plant material. The biomass growth and development of *L. terrestris* were followed during the two seasons. Fluctuations of the population density were mainly caused to the juveniles. Adults had a rather constant abundance during the two years of investigation. Juveniles hatched in late spring and in autumn. *L. terrestris* in the field grew slower than in the laboratory, matured later, reached higher body weight at the onset of maturity but lower maximum adult weight. It is concluded that individuals of *L. terrestris* had to face intense intraspecific competition for food resources in the meadow.
3 ZUSAMMENFASSUNG


Die Konsumrate (C) pro g Regenwurmtrockengewicht pro Woche wurde als nicht-lineare Funktion von Bodentemperatur, Bodenwasserpotential und Nahrungsangebot beschrieben. Optimal für den Konsum war eine Temperatur von ca. 22 °C und ein Bodenwasserpotential von -8.7 kPa. Bei -40 kPa wurde keine Nahrungsaufnahme mehr beobachtet. Der maximale Konsum bei 15 °C war 1.05 (Gras) und 1.23 (Löwenzahn) g Trockengewicht pro g Regenwurmtrockengewicht pro Woche. Für das Berechnen der Konsumrate wurde eine Funktion, welche alle drei Umweltfaktoren berücksichtigt, hergeleitet. Die Assimilationsrate (A) pro g Regenwurmtrockengewicht pro Woche wurde als Summe von Wachstumsrate und Erhaltungsbedarfsrate definiert. Der Erhaltungsbedarf wurde auf der Basis von publizierten Respirationsmessungen berechnet, während das Wachstum gemessen wurde. Hohe Temperaturen und limitierende Umweltfaktoren wie geringes Nahrungsangebot und tiefes Bodenwasserpotential führten zu einer Erhöhung der Assimilationseffizienz (A / C). Bei -8.3 kPa und 15 °C wurden bei Nahrungsangeboten von 0.25 und 1.0 g Löwenzahn Trockengewicht pro g Regenwurmtrockengewicht pro Woche 55 % beziehungsweise 43 % des konsumierten Futters assimiliert.

Die Wachstumsrate pro g Regenwurmtrockengewicht pro Woche war proportional zu dem (Regenwurmtrockengewicht)⁰.⁷⁹. Die Wachstumsrate war bei 23.1 °C, die Entwicklungsrate bei 22.5 °C optimal. Die Juvenilen zeigten bei 20 °C nach 66 d, bei 7.5 °C nach 180 d erste äussere Merkmale der sexuellen Reife (männlich Poren, Tuberculum pubertatis). Das Klitellum begann bei den oben erwähnten Temperaturen nach 82 beziehungsweise 213 Tagen zu wachsen. Das mittlere Trockengewicht von *L. terrestris* bei beginnendem Wachstum des Klitellums war 0.64 g. Die Mortalität während des Juvenilstadiums betrug bei 25 °C 100 % und nahm mit sinkender Temperatur bis zu 0 % bei 7.5 °C ab. Die meisten der Tiere starben während des Stadienwechsels.

Die Reproduktionsrate in g Kokontrockengewicht pro g Regenwurmtrockengewicht pro Woche wurde mit einem Modell mit zwei linearen Bereichen, einem für die steil ansteigende Rate am Anfang der Adultphase, einen zweiten für die langsam sinkende Rate mit zunehmendem Alter, beschrieben. Die maximale Reproduktion wurde bei 15 °C 6.2


4 LIFE CYCLE OF *LUMBRICUS TERRESTRIS* L.

The life cycle of *L. terrestris* includes a cocoon, juvenile and adult stage. Each of these stages has its own functions and attributes. Cocoons are envelopes containing yolk and zygotes. Hatched juveniles grow and develop to sexually mature adults. Once adult, they begin to produce cocoons and continue to grow to a specific body weight limit. Earthworms are generally hermaphroditic and are grouped among semi-continuous/continuous breeders according to OLIVE & CLARK (1978).

Biological processes such as maintenance, growth, development and reproduction of poikilotherm organisms are generally strongly influenced by temperature. Therefore, the residence time of *L. terrestris* in each of the three stages is mainly determined by this factor.

The food demand to sustain the mentioned processes is supposed to depend on temperature and food quality. Until the point of emergence the embryos in the cocoons are supported by the yolk supply. Juveniles and adults, however, have to search for food. The success of this search may depend on environmental factors such as food availability, soil water potential and temperature. Therefore, nutrition is certainly a second important factor influencing the life cycle of *L. terrestris*.

Since the temperature is so important for poikilotherms, one aim is to investigate its influence under otherwise unrestricted conditions on the three stages (chapters 4.2 and 4.3). Additionally, limits imposed on the nutrition by several environmental factors such as temperature, soil water potential and the amount of food available are studied in chapter 4.1.

Rates of consumption, assimilation, maintenance, growth and reproduction have been calculated per g earthworm dry weight and per week. The dependency of the rates on environmental factors was described quantitatively by mathematical functions. The symbol "wk" has been used throughout the work to designate "week".
4.1 DRY MATTER CONSUMPTION AND ASSIMILATION BY JUVENILES UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

The importance of the food quality for the consumption of *Lumbricus terrestris* has been extensively demonstrated by SATCHELL & LOWE (1967), ZICSI & POBOZSNY (1977) and ZICSI (1983). The significance of other factors, such as soil temperature, soil water potential and food amount available has not yet been quantified. The goal of this study is to evaluate the influence of soil temperature, soil water potential, and the amount of food offered on food consumption and assimilation by juveniles of *L. terrestris*.

Part of the ingested food is digested and resorbed, and assimilates are used to sustain several processes such as maintenance, growth and reproduction. Depending on the process to which assimilates are allocated, they are converted into energy, body tissue and offspring. Conversion efficiencies may be different according to the processes considered. As reproductive animals are not investigated in this study, the sum of growth and maintenance, defined as assimilation, was assumed to be a function of consumption. Maintenance could be calculated based on respiratory measurements reported in the literature, whereas growth had to be measured.

4.1.1 Material and methods

Experiments

Juvenile *L. terrestris*, with live weights ranging from 0.5 to 3.5 g, were collected from a meadow near the Swiss Federal Research Station for Farm Management and Agricultural Engineering in Tänikon using 0.005 % chloroacetophenone (CN) solution (chapter 5.1). Earthworms were then kept at least one week at 10 °C in soil with a water content of 40 % and with dandelion (*Taraxacum officinale*) ad libitum as food.

The soil (clayey loam) used for rearing originated from the lower part of the A-horizon of the same meadow. After drying the soil slightly, it was crumbled by hand, sieved (5 mm mesh) and moistened to the desired water content level. The corresponding water potentials were estimated in boxes prepared as those used in the experiments by means of tensiometers (2 measurements per moisture level). Dandelion and grass, also collected in the Tänikon meadow, were used as food. These were dried for 3-4 h at 60 °C immediately after harvesting. Soil and food for the experiments were stored at 2 °C.

The experiments were carried out in climatic chambers. Worms were kept in the darkness separately in cylindrical polyethylene-boxes (diameter: 10 cm, height:
12 cm) with perforated lids. Each box contained 150 g (dry weight) soil, which had been slightly firmed. The water content was adjusted to 40 % (water potential: -8.7 kPa), except where otherwise noted. Duration of the experiments was one week.

Immediately before the experiments started the food was dried again for 3 h at 60 °C. The dandelion leaves were cut into pieces of about 1 cm², grass to a length of 1 - 2 cm. Food was placed on the soil surface once at the beginning of the experiments. The amount of food added was 40 % of the live weight of the earthworms, unless otherwise noted. The live weight of the earthworms was determined after rinsing them in cold tap water and blotting them with filter paper.

At the end of the experiments, the remaining food was removed and gently rinsed in tap water to eliminate soil particles; its weight was measured after drying it for 24 h at 105 °C. The live weight of the earthworms was measured again; the dry weight was assessed after drying the earthworms for 24 h at 105 °C.

The following experiments on food consumption and assimilation by earthworms were carried out:

Experiment 1 was conducted to measure the loss in weight of food due to extraction and decomposition in the absence of earthworms. 70 boxes were prepared with 0.4 g food on the soil surface. 40 boxes were incubated at 7.5, 10.0, 12.5, 15.0, 17.5, 20.0, 22.5 or 25.0 °C. The remaining 30 boxes were all incubated at 15 °C, but had soil water contents of 28, 32, 36, 40, 44 or 48 %. Each condition was tested with 5 replicates, i.e. 5 boxes for each temperature and for each water content treatment.

Experiment 2 was carried out to investigate the influence of temperature. 70 boxes, each containing one juvenile, were incubated at 7.5, 10.0, 12.5, 15.0, 17.5, 20.0 or 25.0 °C, with 10 replicates per temperature.

Experiment 3 was executed to investigate the influence of soil moisture. 60 boxes, each containing one juvenile, were kept at 15 °C, and had soil water contents of 28, 32, 36, 40, 44 or 48 %. Each moisture level had 10 replicates.

Experiment 4 and 5 were accomplished to examine the influence of food availability. 100 boxes, each containing one juvenile, were kept at 15 °C. Dandelion was given as food in experiment 4, grass in experiment 5. Food was provided at 0, 5, 10, 20 or 40 % of individual worm biomass each replicate using 10 replicates per treatment.
Analysis of experiments

Estimation of weight

To simplify the evaluation of the results and ameliorate their transferability, a function was needed that would describe the dry weight of juvenile *L. terrestris* in relation to live weight and environmental factors. The data on live and dry weights of *L. terrestris* obtained at the end of experiments 2, 3 and 4 were used to perform a multiple regression analysis (by the method of least squares) with the model described in equation [1]:

\[
W = W_l \left( b_0 + \sum_{i=1}^{3} (b_i E_i) \right) \quad [1]
\]

where

- \( W \): dry weight in g,
- \( W_l \): live weight in g,
- \( b_0 \): partial regression coefficient for \( W_l \),
- \( i \): \( i = 1 \): temperature (T \(^\circ\)C); \( i = 2 \): negative value of soil water potential (-P [kPa]); \( i = 3 \): food offered (F [g g\(^{-1}\) wk\(^{-1}\)]),
- \( b_i \): partial regression coefficient for the interaction terms,
- \( E_i \): environmental factors (T, P, F).

Factors whose partial regression coefficients were not significantly (\( \alpha = 0.05 \)) different from zero were removed in a step-wise procedure as suggested by ZAR (1984). This function was subsequently used to transform all measured live weights of *L. terrestris* into dry weights.
Estimation of food consumption (C)

The weekly consumption was calculated with equation [2]:

\[
C = \frac{A - B (1 + L)}{W}
\]  

[2]

where

\(C\): consumption [g g\(^{-1}\) wk\(^{-1}\)],
\(A\): dry weight in g of the food offered (0.95 x weight measured at 60 °C),
\(B\): dry weight in g of the remaining food after one week,
\(L\): fraction of the remaining food, which was lost through extraction or microbial activity,
\(W\): dry weight in g of \(L.\ terrestris\), calculated as the mean of the initial dry weight (calculated according to equation [1]) and the final dry weight (measured).

The loss of a fraction of the remaining food (microbial respiration, incomplete extraction) was considered in the calculation of the weekly consumption with equation [3]:

\[
L = b_0 + \sum_{i=1}^{2} (b_i E_i)
\]  

[3]

where

\(L\): fraction of the remaining food, which was lost through extraction or microbial activity,
\(b_0\): intercept,
\(i\): \(i = 1\): temperature (T [°C]); \(i = 2\): negative value of soil water potential (-P [kPa]),
\(b_i\): partial regression coefficient for the environmental factors \(i\),
\(E_i\): environmental factor (T, P).

Data from experiment 1 were used to estimate the parameters \(b_0\) and \(b_i\) of equation [3] by means of a least square multiple linear regression analysis.

Consumption as a function of environmental conditions

Empirical equations were used to fit the weekly food consumption (C) in experiment 2 and 3 at different levels of temperature [equation 4] and soil water potential [equation 5], respectively:
\[ C(T) = a_1 (28 - T)^{a_2} \exp(-a_3 (28 - T)) \quad \text{for } T \leq 28 \, ^\circ C \]  

and

\[ C(P) = a_1 (-P + 10)^{a_2} \exp(-a_3 (-P + 10)) \quad \text{for } P \leq 0 \, \text{kPa} \]

where

- \( C(T) \): consumption \([g \, g^{-1} \, wk^{-1}]\) as a function of temperature (T),
- \( C(P) \): consumption \([g \, g^{-1} \, wk^{-1}]\) as a function of soil water potential (P),
- \( T \): temperature in \(^\circ C\),
- \( P \): soil water potential in \(\text{kPa}\),
- \( a_1, a_2, a_3 \): parameters of the function.

The weekly consumption was assumed to be zero at zero values of temperature and soil water potential. Both are justified because there is evidence that no earthworm activity occurs below \(0 \, ^\circ C\) (Kollmannspurger, 1955), and that water saturation, causing oxygen depletion, presumably has detrimental effects on earthworms. Wolf (1938) found the upper lethal temperature limit for \(L. \, terrestris\) to be from 27.5 - 28.5 \(^\circ C\). Therefore, it is assumed in equation [4] that no consumption occurred at temperatures higher than 28 \(^\circ C\).

The estimated values of the consumption of dandelion and grass at varying levels offered were fitted with equation [6]:

\[ C(F) = a_1 \left(1 - \exp(-a_2 F)\right) \]

where

- \( C(F) \): consumption \([g \, g^{-1} \, wk^{-1}]\) of dandelion or grass as a function of food offered (F),
- \( F \): offered food \([g \, g^{-1} \, wk^{-1}]\) (dandelion, grass) as proportion of the earthworms dry weight,
- \( a_1, a_2 \): parameters of the function.

Parameter \(a_1\) represents the maximum food consumption if food is supplied in excess, \(a_2\) determines how fast this maximum occurs.

General consumption function

In the experiment 2, soil water potential (P) and quantity of food offered (F) were assumed to be non-limiting for food consumption. Hence, equation [4] describes the maximum consumption at a given temperature. Scalars were defined to account for the
influence of both the amount of food offered and the soil water potential on food consumption (equation [7]):

$$\text{C}(T, P, F) = \text{C}(T) \cdot \text{c}_{p} \cdot \text{c}_{f}$$ \hspace{1cm} [7]

where

- \( \text{C}(T, P, F) \): consumption \([\text{g} \cdot \text{g}^{-1} \cdot \text{wk}^{-1}]\) as a function of \(T\) (temperature), \(P\) (soil water potential) and \(F\) (food offered),
- \( \text{C}(T) \): consumption \([\text{g} \cdot \text{g}^{-1} \cdot \text{wk}^{-1}]\) as a function of \(T\),
- \( \text{c}_{p} \): scalar, accounting for water potential limitations,
- \( \text{c}_{f} \): scalar, accounting for food limitations.

The scalars accounting for the effect of both the amount of food offered and the soil water potential on food consumption were defined in equations [8] and [9]:

$$\text{c}_{p} = \frac{\text{C}(P)}{\text{C}(P_{\text{opt}})}$$ \hspace{1cm} [8]

where

- \( \text{c}_{p} \): scalar, accounting for water potential limitations,
- \( \text{C}(P) \): consumption \([\text{g} \cdot \text{g}^{-1} \cdot \text{wk}^{-1}]\) at prevailing water potential,
- \( P_{\text{opt}} \): soil water potential, at which maximum consumption was observed (this corresponds to \(-\frac{a_{2}}{a_{3}}\), parameters being from equation [5] (first derivative equals zero)),

and

$$\text{c}_{f} = \frac{\text{C}(F)}{a_{1}}$$ \hspace{1cm} [9]

where

- \( \text{c}_{f} \): scalar, accounting for food limitations,
- \( \text{C}(F) \): consumption \([\text{g} \cdot \text{g}^{-1} \cdot \text{wk}^{-1}]\) at prevailing food availability,
- \( a_{1} \): parameter from equation [6], representing the maximum food consumption, if food is supplied in excess.

### Food Assimilation (A)

The model in equation [10] assumes that assimilation (A) is allocated to growth (G) and maintenance (M), and is a function of consumption (C):
where

\[ \begin{align*}
A &= G + M(T, W) = C \left( b_0 + \sum_{i=1}^{3} (b_i E_i) \right) \\
M(T, W) &= \text{maintenance costs for basal metabolism} \ [g \ \text{g}^{-1} \ \text{wk}^{-1}] \ \text{(calculated)} \\
C &= \text{consumption} \ [g \ \text{g}^{-1} \ \text{wk}^{-1}] \ \text{(measured and corrected for extraction and microbial decomposition losses),} \\
b_0 &= \text{partial regression coefficient for } C, \\
E_i &= \text{environmental factors} \ (T, P, F).
\end{align*} \]

\[ A, G, M \text{ and } C \text{ are in rates per week and } g \ \text{earthworm biomass. The growth of juveniles is calculated as the difference between the dry weight at the beginning and at the end of the experiments, whereas the maintenance costs were estimated from respiration measurements reported in the literature. Assuming that } 1 \ \text{ml oxygen corresponds to } 20.09 \ \text{J } \left( \text{CZIHAK et al., 1976} \right), \text{ and that } 1 \ \text{g earthworm biomass} \ \text{(dry weight)} \ \text{equals } 17209 \ \text{J } \left( \text{BOLTON & PHILLIPSON, 1976} \right), \text{ the loss of assimilates due to respiration could be calculated. The oxygen consumption in one hour at } 19^\circ \text{C as a function of the live weight was measured by BYZOVA (1965). Her function was modified to account for the dry weight of earthworms. Thereafter, the weekly oxygen consumption per } g \ \text{dry weight of earthworm biomass was calculated according to equation} \ [11]:
\]

\[ M(T, W) = \frac{20.09}{17209} k(T) h A W^{b^{-1}} \]

\[ \begin{align*}
M(T, W) &= \text{maintenance costs for basal metabolism} \ [g \ \text{g}^{-1} \ \text{wk}^{-1}] \ \text{depending on temperature} \ (T) \ \text{and weight of the earthworms} \ (W), \\
k(T) &= \text{function, accounting for the influence of temperature on oxygen consumption}, \\
h &= \text{hours per week } (= 168), \\
A &= \text{oxygen consumption in one hour per unit of weight } (= 83.5), \\
f(\cdot) &= \text{dry weight proportion of a live } L. \ \text{terrestris, depending on environmental factors (equation} \ [1]), \\
W &= \text{dry weight in } g \ \text{of } L. \ \text{terrestris, calculated as the mean of the initial dry weight} \ \text{(calculated according to equation} \ [1]) \ \text{and the final dry weight} \ \text{(measured)}, \\
W_i &= \text{live weight in } g, \\
b &= \text{factor, showing the influence of the weight on respiration } (= 0.78).}
\]
The influence of the temperature is included in equation [11] with a function \( k(T) \), which was built on the findings of POMERAT & ZARROW (1936) (equation [12]):

\[
k(T) = \exp \left( \frac{\mu}{R} \left( \frac{1}{292} - \frac{1}{273 + T} \right) \right)
\]

where

- \( k(T) \): function, accounting for the influence of temperature on oxygen consumption,
- \( \mu \): constant of the Arrhenius equation (11040),
- \( R \): gas constant (1.9872),
- \( T \): temperature in °C.

The assimilation (A) for each earthworm could then be calculated and the parameters \( b_0 \) and \( b_1 \) in equation [10] were estimated by a least square multiple linear regression analysis.

### 4.1.2 Results and discussion

The following results are all presented on a dry weight basis, but dry weights could easily be transformed into energy. BOLTON and PHILLIPSON (1976a) found that one g (dry weight with ash) \( L. \) terrestris is equivalent to 17.209 kJ, 16.649 kJ and 21.849 kJ for juveniles, adults and cocoons, respectively. CUENDET (1985) estimated for a sample of juvenile and adult \( L. \) terrestris with voided guts 21.98 kJ per g dry weight. As in this study dry weights are measured of earthworms with unvoided guts, the figures of BOLTON and PHILLIPSON (1976a) should be used for transformations. Our own bomb calorimetric measurements (\( n = 2 \)) with dandelions came to 17.98 kJ energy equivalents per g dry weight.

Zero earthworm mortality was recorded during the week before the beginning of the experiments. One juvenile died in experiment 5. Three earthworms in experiments 2, 3 and 4 had superficial injuries and one seemed to have lost some of posterior segments at the end of the experiment. Nevertheless, all earthworms, except the dead one, were included in the statistical analysis.

**Dry weight**

Temperature was the only environmental factor influencing significantly (\( \alpha = 0.05 \)) the dry weight / live weight relationship. The partial regression coefficients \( b_0 \) and \( b_1 \) (tab. 1) were significantly different from zero (\( p < 0.0005 \)) and the squared multiple R was equal to 0.991. As \( b_1 \) is the partial regression coefficient of the interaction term
W \times T, the water content of *L. terrestris* is lowered at both high temperatures and high live weights. As behavior of *L. terrestris* is age specific (juveniles: epigean; adults: living in deep burrows), it seems reasonable, that water balances is weight dependent. According to equation [1] 1 g earthworm (live weight) will have a water content of 81.6 % at 5 °C and 78.19 % at 25 °C. This is in contrast to findings of KUDRJASEVA (1987), who found *Eisenia nordenskioeldi* (EISEN) to have lower body water contents in winter than in summer at comparable soil water contents. But since her winter measurements were conducted at a temperature of -1 °C, the observed lower water content may reflect the reaction of this soil litter inhabiting species to freezing conditions. CARLEY (1978) found 77 % water content if *L. terrestris* were acclimatized to moist soil, 87 % if they were acclimatized to pond water. KUDRJASEVA (1982) observed notable seasonal variations of the live weight due to partial dehydration of *E. nordenskioeldi* sampled in a forest. Thus the live weight of earthworms is highly variable and equation [1] does not explain the full range of possible hydration states of *L. terrestris*. It may be, that the soil-water regime has the most important influence on the earthworm body-water content. KRETZSCHMAR (1989) showed that with different soil types only pF values greater than 2.55 (-35.5 kPa) had effects on the water content of the earthworm *Aporrectodea longa* (UDE). The soil water potential in the range of -3 to -40 kPa, as chosen in the experiment 3, was probably too small to demonstrate effects of dry soil conditions on the water content of *L. terrestris*.

Estimation of food consumption (C)

Equation [3] describes the proportion of food that disappears in the absence of earthworms through the activity of microorganisms or the extraction procedure. In this model the partial regression coefficients b₀, b₁ and b₂ (tab. 1) were significantly different from zero (p < 0.0005) and the regression explained 76 % of the variance.

**Tab. 1:** Partial regression coefficients of the multiple linear regressions (equations [1, 3 and 10]). Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>equation</th>
<th>b₀</th>
<th>b₁</th>
<th>b₂</th>
<th>b₃</th>
</tr>
</thead>
<tbody>
<tr>
<td>[1]</td>
<td>0.1756</td>
<td>0.0017 (0.0004)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>[3]</td>
<td>0.1062</td>
<td>0.0190 (0.0014)</td>
<td>-0.004 (0.001)</td>
<td></td>
</tr>
<tr>
<td>[10]</td>
<td>0.5009</td>
<td>0.0035 (0.0019)</td>
<td>0.004 (0.002)</td>
<td>-0.1556 (0.0165)</td>
</tr>
</tbody>
</table>
High temperatures and high water potentials increased the proportion of food lost when no earthworms were in the experimental boxes. A correction of the food consumption using equation [2] is merely an approximation, as the amount of food offered as well as the earthworm/microbial interactions are not included in the model.

Consumption as a function of environmental conditions

Food consumption increased with rising temperature, but decreased above a temperature of about 21 °C (fig. 1). The estimated parameters of the fitted curve are given in tab. 2. The shape of the curve reflects increasing uptake of food, needed to meet the requirements for basal maintenance and growth with rising temperatures, and an upper thermal threshold for food processing and metabolism.

Daily consumption rates measured by several authors were transformed for comparison to weekly rates based on the earthworms dry weight (assuming a water content of \textit{L. terrestris} of 80 %). CURRY et BOLGER (1984) estimated at 15 °C a consumption of 0.735 g g\(^{-1}\) wk\(^{-1}\) of willow (\textit{Salix aquatica cv. gigantea} ), whereas SHIPITALO et al. (1988) measured a consumption of 0.07 to 0.455 g g\(^{-1}\) wk\(^{-1}\) at 15 °C with several plant species of agricultural importance. These data are lower than those reported in fig. 1. With litter from several deciduous trees in different degrees of decomposition ZICSI (1983) found consumption rates ranging from 0 to 1.393 g g\(^{-1}\) wk\(^{-1}\) at 10 °C. The consumption rates observed by ZICSI (1983) are probably overestimated, because his measurements were based on air-dried plant materials. His measurements suggest, nevertheless, that consumption of plant materials may exceed the quantity observed for dandelion, depending on species and decomposition state.

The dependency of the food consumption on the soil water potential is shown in fig. 2. The sharp decline in the consumption rate near water saturation is not supported by measurements, but is assumed to occur due to oxygen depletion in the soil. At higher soil water potentials the consumption rate decreased. The influence of the soil water potential on consumption seems to be more important than on the water content of \textit{L. terrestris}. It is supposed, that soil water potential (perhaps rather soil plasticity) is an important factor in food processing. The building of deep burrows enables \textit{L. terrestris} to locate mineral soil with the needed soil water potential even though the soil surface is dry. During short summer thunderstorms water may infiltrate the soil predominantly through macropores with openings to the surface (BEVEN and GERMANN, 1982), such as earthworm channels, bypassing capillary flow through the soil matrix. Thus, even if the soil is dry in deeper layers, water conducted down their burrows probably allow \textit{L. terrestris} to feed for short periods.
Food consumption increases with higher food availability, but only up to a certain extent (fig. 3). The shape of the curve fitted to the data (equation [6]) corresponds to a functional response curve of type 2. The parameter $a_1$ determines the level of the plateau and $a_2$ how fast the maximum is reached. Although dandelion and grass may have different physical and chemical qualities, the maximum consumption of both (1.054 g g$^{-1}$ wk$^{-1}$, 1.235 g g$^{-1}$ wk$^{-1}$) was very similar (tab. 2).
**Tab. 2**: Parameters $a_1$, $a_2$ and $a_3$, estimated for the curve fitting functions (equations [4, 5 and 6]). Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>equation</th>
<th>$a_1$</th>
<th>$a_2$</th>
<th>$a_3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>[4]</td>
<td>0.515 (0.133)</td>
<td>1.840 (0.262)</td>
<td>0.297 (0.036)</td>
</tr>
<tr>
<td>[5]</td>
<td>0.136 (0.096)</td>
<td>0.657 (0.199)</td>
<td>0.009 (0.002)</td>
</tr>
<tr>
<td>[6]</td>
<td>1.054 (0.166)</td>
<td>1.216 (0.306)</td>
<td></td>
</tr>
<tr>
<td>(dandelion)</td>
<td>1.235 (0.100)</td>
<td>1.018 (0.154)</td>
<td></td>
</tr>
<tr>
<td>[6]</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**General consumption function**

With equation [7] a general consumption function could be constructed based on the equations [4, 5 and 6] and parameters in tab. 2. For the calculation of the scalars $c_p$ and $c_1$ (equations [8 and 9]) the maximum consumption in experiments 3 and 4 had to be known. According to equation [4] the calculated consumption at 15 °C was 1.215 g g$^{-1}$ wk$^{-1}$. In experiment 4 the consumption was 1.181 g g$^{-1}$ wk$^{-1}$ at an optimum soil-water potential of -7.3 kPa (first derivative of equation [5] equals zero). Fig. 4 illustrates the influence of temperature and the soil water potential at non limiting food supply on food consumption.

There was some evidence from the data that the consumption rate may also be weight dependent. DICKSCHEN and TOPP (1987) observed the same phenomenon for the earth-
worm *Lumbricus rubellus* HOFFMEISTER with alder (*Alnus* sp.) leaves as food. Because the earthworms were chosen randomly for all the experimental conditions, it is to be expected that no systematic error is introduced and the found general consumption function holds for *L. terrestris* with a mean body weight equal to those animals used in experiment 2. If subsequent studies prove an influence of the body weight on the consumption rate, an additional term accounting for the body weight dependency of consumption may be introduced into the general consumption function given in this work.

**Food assimilation (A)**

The calculated maintenance costs (M) at 15 °C depend on the weight of the earthworms and ranged for those used in the experiments from 4.5 to 7.3 % of the body weight per week. Q_{10} values in the temperature range under consideration were between 1.91 and 1.98 (equation [12]). Smaller animals than those used in the experiments are assumed to require considerably more energy to meet the demand for basal maintenance. A freshly hatched juvenile with a wet weight of about 0.05 g, for example, requires, according to equation [11], an equivalent of about 15.2 % of his body dry weight per week at 15 °C. Thus, at high temperatures and under conditions of low food availability, starvation may contribute to the mortality of small juveniles.

Assimilation, calculated as the sum of growth (G) and maintenance (M) according to equation [10], did not depend linearly on consumption (C). Not only the partial regression coefficient for C (p = 0.000), but also the regression coefficients for the interaction terms (tab. 1) in equation [10] were significantly different from zero. Significance-values for the interaction terms were 0.061, 0.000 and 0.021 for temperature, food availability, and soil water potential, respectively. The regression explained 89.3 % of the variance. The most important environmental factor was food availability (F). Juveniles assimilated more at low food availability than at non-limiting food conditions. For example, it was calculated that at -8.3 kPa and at 15 °C they assimilate 55 and 43 % of the ingested dandelion if food availability was 0.25 and 1.0 g g⁻¹ wk⁻¹, respectively. It may be that food exploration is enhanced by coprophagy or grazing on the microflora growing on the faeces, if food is in shortage. With increasing temperature and decreasing soil water potential the assimilation increased. Since food consumption nearly stops below -50 kPa (fig. 2), assimilation is only affected over a limited range by the soil water potential. It seems that high temperature and restricting environmental conditions, such as low food availability and low soil water potential, lead to an increase in the assimilation efficiency (A / C) of *L. terrestris*.
Fig. 4: Consumption of dandelion leaves by juvenile *Lumbricus terrestris* at different soil water potentials and temperatures as predicted by the general consumption function (equation [7]). Consumption is calculated as g leaf dry weight per g earthworm dry weight per week.

DICKSCHEN and TOPP (1987) found that the epigean species *L. rubellus* digested 69 and 76 % of ingested alder leaves at 15 and 5 °C, respectively. Assuming conversion costs of 20 % of the digested material, the alder leaf assimilation was 55 to 61 % of the ingested food. A similarly high dandelion assimilation by *L. terrestris* could only be expected at very low food availabilities. LEE (1985), based on data of BOLTON & PHILLIPSON (1976b) and LAVELLE (1974), calculated daily energy budgets. For the endogean species *Aporrectodea rosea* (SAVIGNY) in an English beech forest assimilation by adults and small immatures were only 1.3 % and 2.8 % of the ingested organic matter, respectively. For a population of geophageous Megascoleidae and Eudrilidae from a savanna ecosystem at Lamto, Ivory Coast, he estimated that 8.9 % of the consumed food were assimilated. Therefore, geophageous species are assumed to be relatively inefficient in comparison with the litter feeding earthworms *L. terrestris* and *L. rubellus*. 

4.2 GROWTH AND MATURATION OF JUVENILES

Growth and development of the poikilotherm earthworms, as described in MICHON (1954), LOFS-HOLMIN (1982), HARTENSTEIN & AMICO (1983), are mainly influenced by temperature. Other environmental factors such as food availability (CURRY & BOLGER, 1984), food quality (ZICSI & POBOZSNY, 1977; BOSTRÖM & LOFS-HOLMIN, 1986; BOSTRÖM, 1987; BOSTRÖM, 1988) and soil water potential (LAVELLE, 1974) also influence growth and development.

It is assumed that growth depends not only on environmental factors, but also on the body weight of the animals. The dependency of the growth on the body weight of *Lumbricus terrestris* was not studied up to date. Growth as well as body weight and age of *L. terrestris* with incipient external signs of maturity (MICHON, 1954; LOFS-HOLMIN, 1982) was only measured in relation to few fixed temperatures.

The aim of this study is to develop a mathematical model which describes the growth rate of *L. terrestris* as a function of its body weight and temperature, and the development rate as a function of temperature. Furthermore, body weight and age of *L. terrestris* with incipient external signs of maturity were determined.

4.2.1 Material and methods

Experiment

Freshly hatched juveniles of *L. terrestris* were collected daily from cocoons produced from laboratory cultures. They were stored at 5 °C and used within a week. Soil for the experiment originated from the *A*-horizon of a meadow near the Swiss Federal Research Station for Farm Management and Agricultural Engineering in Tänikon (chapter 4.1.1). After drying the soil slightly, it was crumbled by hand, sieved (5 mm mesh) and re-moistened to a water content of 40%. Leaves of dandelion (*Taraxacum officinale*), also collected in the Tänikon meadow, were dried for 3 - 4 h at 60 °C immediately after harvesting. Thereafter, they were stored at 2 °C.

The experiment was carried out in constant temperature rooms. Individual worms were placed in cylindrical polyethylene boxes (diameter: 10 cm, height: 12 cm) containing 450 g (dry weight) slightly firmed soil. The boxes were covered by perforated lids. Batches of 20 boxes were placed in a covered plastic box, in which a 1 cm water layer on the floor helped maintain high air humidity. Food (dandelion pieces of about 1 cm²) was provided *ad libitum* and added to the boxes every week.
Freshly hatched juveniles were incubated at 7.5, 10.0, 12.5, 16.0, 17.5, 20.0, 22.5 or 25.0 °C. Each condition was tested with 20 replicates (one batch), except 7.5 °C with 8.

The live weight of the earthworms was determined after rinsing them briefly in tap water and blotting them with filter paper. At the beginning of the experiment their weight was measured every 4 or 5 weeks. When earthworms had about 2 g live weight, they were observed more frequently and the age, and body weight, were recorded when the male pores appeared as well as when the clitellum began to grow. At this stage the experiment was terminated. The clitellum was assumed to start growing when its diameter (contracted individuals) became larger than that of the earthworm's body. The smallest time interval between measurements was one week. This procedure allowed an estimation of the age and weight of *L. terrestris* with incipient external signs of maturity.

**Analysis of experiments**

**Growth**

Equation [13], which is given in chapter 4.1, was used to transform the measured live weights of *L. terrestris* into dry weights:

\[ W = W_l (0.1756 + 0.0017 T) \]  \[ 13 \]

where

- \( W \): dry weight [g],
- \( W_l \): live weight [g],
- \( T \): temperature [°C].

Only measurements from individuals without any sign of maturity (male pores, tuberculum pubertatis, clitellum), and for which the time intervals between measurements were 4 or 5 weeks, were used in the growth rate calculations. Earthworms kept at 25 °C were not included in the growth rate analysis, since they all died before transition between stages. Thus, a total of 352 growth rates at different temperatures and body weights of *L. terrestris* were calculated with with equation [14]:


\[ \Delta G = \frac{W_1 - W_0}{\Delta t \left( \frac{W_1 + W_0}{2} \right)^{0.5}} \]  

where

- \( \Delta G \): growth rate \([g \, g^{-1} \, wk^{-1}]\),
- \( W_0 \): dry weight \([g]\) at the beginning of a time interval \(\Delta t\),
- \( W_1 \): dry weight \([g]\) at the end of a time interval \(\Delta t\),
- \( \Delta t \): time interval \([wk]\).

Several linear and nonlinear functions (JOHNSON & THORNLEY, 1985; RATTE, 1985; LOGAN, 1988) are known to describe the temperature dependency of biological process rates. The nonlinear function named type III in LOGAN (1988) (equation [15]) was used here to describe the temperature dependency of the rate of growth as well as of the development, since its descriptive attributes are most adequate to the low deviation of the data from nonlinearity in the low temperature range and to a rapid decline of the rate at temperatures higher than the optimum:

\[ r = \psi \left( \frac{(T - T_{\text{min}})^2}{(T - T_{\text{min}})^2 + D^2} \right) \cdot \exp\left( \frac{T_{\text{max}} - T}{T_{\text{max}} - T_{\text{opt}}} \right) \]  

where

- \( r \): temperature dependent rate of development \([wk^{-1}]\),
- \( \psi \): maximum rate of development \([wk^{-1}]\) possible,
- \( T \): temperature \([^\circ C]\),
- \( D \): empirical constant,
- \( T_{\text{min}} \): base temperature \([^\circ C]\),
- \( T_{\text{opt}} \): temperature \([^\circ C]\) at which maximum rate occured,
- \( T_{\text{max}} \): upper threshold temperature \([^\circ C]\).

Assuming that the rate \( r \) in equation [15] is the growth rate \( \Delta G \), and that the maximum rate possible (\( \psi \)) scales as \( W^{b-1} \), growth rate as a function of temperature and the dry weight of the earthworms is described by equation [16]:
\[ \Delta G = a W^{b-1} \left( \frac{(T-T_{\text{min}})^2}{(T-T_{\text{min}})^2+D^2} \right) \exp \left( \frac{T_{\text{max}}-T}{T_{\text{max}}-T_{\text{opt}}} \right) \]  

[16]

where

\[ \Delta G: \quad \text{growth rate [g g}^{-1} \text{ wk}^{-1}] \text{ as a function of the body dry weight and the temperature,} \]
\[ W: \quad \text{dry weight [g] of } L. \text{ terrestris,} \]
\[ a: \quad \text{parameter of the function,} \]
\[ b: \quad \text{factor, showing the dependency of growth on weight.} \]

The parameters of this function were estimated by the method of least squares. \( T_{\text{min}} \) was set to zero.

**Body weight at maturity**

One-way analyses of variance (ZAR, 1984) were performed to test whether or not temperature had an influence on the body weight of \( L. \) terrestris with incipient male pores and incipient clitellum growth. The mean dry weights of dandelion- and grass-fed animals (both kept at 16 °C) were compared with a two-way t test (ZAR, 1984).

**Age at maturity**

Earthworms change their external morphology before they reach sexual maturity. In \( L. \) terrestris male pores appear first in segment 15 and tubercula pubertatis develop along the ventral border of the clitellum, and finally the saddle shaped clitellum grows in the segments 32-37. The clitellum is fully developed at the time oocytes are released in the ovisacs (OLIVE & CLARK, 1978). The begin of the clitellum growth is closer to the onset of sexual maturity than the appearance of male pores, but is less precisely observed. Nevertheless, development rates were calculated at each temperature by taking the reciprocal values of the age of \( L. \) terrestris with incipient clitellum growth. Equation [15] was used to describe the temperature dependency of the development rate. The rates \( r \) and \( \psi \) in equation [15] were in \( \text{wk}^{-1} \). The parameters of this equation were estimated by the method of least squares.

**Mortality**

Mortality of \( L. \) terrestris was calculated as percent of the animals dying before male pores became visible as well as before the clitellum commenced growing.
4.1.2 Results and discussion

Growth

The growth rate of *L. terrestris* is body weight and temperature dependent (fig. 5). Parameter estimates of equation [16], which describe growth rates at different weights and temperatures, are given in tab. 3. Growth rates, as with respiration, were expressed as a power function $W_{b}^{-1}$, where $W$ is the dry weight and $b$ is a constant. The estimated value of $b$ (0.78) was close to that measured by BYZOVA (1965) for the respiration of *L. terrestris* (0.71). This indicates that growth and respiration may be limited by similar constraints (e.g. surface weight-ratio). SIBLY & CALOW (1986) argued that body weight has several constraints on key metabolic processes. Feeding, food assimilation and the performing of various functions may decline with increasing body weight. Earthworm performances, such as burrowing, organic matter incorporation into the soil, casting and generally speaking amelioration of soil fertility, probably follow the same empirical relationship. Hence, body weight as a structuring element of populations should be taken into account in investigations on earthworm performances in the field. Another conclusion is that using cohorts of earthworms with as similar weights as possible should considerably diminish the variances in laboratory experiments.

Equation [16] can only be used for juveniles. In fact, according to it, the growth rate can never reach zero at temperatures above 0°C, and animals never stop growing. However, *L. terrestris* reaches maximum body live weights between 5.35 and 13.07 g (MICHON, 1954; MEINHARDT, 1974; chapter 4.3).

The optimum temperature for growth ($T_{\text{opt}}$) is 23.1 °C (tab. 3). Since mortality increases with rising temperature (tab. 6), the optimum temperature with respect to fitness is certainly lower than that for growth.

<table>
<thead>
<tr>
<th>a</th>
<th>b</th>
<th>D</th>
<th>$T_{\text{opt}}$</th>
<th>$T_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>0.79</td>
<td>11.4</td>
<td>23.1 (0.26)</td>
<td>24.4 (0.83)</td>
</tr>
</tbody>
</table>

Tab. 3: Parameters a, b and D and optimum ($T_{\text{opt}}$) and maximum ($T_{\text{max}}$) temperature estimated for the curve fitting function of the growth rate (equation [16]). Standard errors are given in brackets.
Tab. 4: Parameters $a$, $b$ and $D$, and minimum ($T_{\text{min}}$), optimum ($T_{\text{opt}}$) and maximum ($T_{\text{max}}$) temperature estimated for the curve fitting function of the development rate (equation [15]). Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>$\psi$</th>
<th>D</th>
<th>$T_{\text{min}}$</th>
<th>$T_{\text{opt}}$</th>
<th>$T_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1294</td>
<td>15.4 (0.038)</td>
<td>-0.5 (0.16)</td>
<td>22.5 (0.10)</td>
<td>22.5 (0.07)</td>
</tr>
</tbody>
</table>

Fig. 5: Growth rate in body dry weight per week (wk) of *Lumbricus terrestris* as predicted by the model (equation [16]) for different body dry weights and temperatures.

**Body weight at maturity**

Mean dry weights and standard deviations at different temperatures for dandelion-fed *L. terrestris*, shortly after they developed male pores or a clitellum, are shown in fig. 6. A one-way analysis of variance proved that temperature significantly ($p = 0.004$) influences the weight of individuals up to the appearance of the male pores. For animals with incipient clitellum growth the influence of temperature on the weight was not significant ($p = 0.223$). The dry weight of all surviving *L. terrestris* with incipient male pores was $0.47 \pm 0.085$ g ($n = 101$), that of *L. terrestris* with incipient clitellum growth was $0.64 \pm 0.113$ ($n = 79$). At 16 °C the mean dry weight of *L. terrestris* with incipient male pores fed with grass ($0.44 \pm 0.062$ g) was lower than that of animals
fed with dandelion (t test, p = 0.015). The difference in the dry weight of grass-fed earthworms with incipient clitellum growth (0.62 ± 0.078) as compared with those fed with dandelion was less obvious (t test, p = 0.076).

One can postulate that in *L. terrestris* body weight at maturity is not constant, but is influenced by temperature and food.

It may be that the body weight at maturity is influenced at least partly by the gonadal weight, as is known for insect females (e.g. RATTE, 1985). Another explanation would be that the onset of maturation is influenced by the environmental condition dependent amount of reserves, such as fat, stored in the body.

---

**Fig. 6:** Dry weights of *Lumbricus terrestris* with incipient male pores (dark bars) and with incipient clitellum growth (grey bars) (Means and standard deviations).

**Fig. 7:** Development rates of *Lumbricus terrestris* with incipient clitellum growth (Means and standard deviations).

---

**Age at maturity**

The duration from hatching until the development of male pores as well as of the clitellum is shown in tab. 5. It has been shown by LOFS-HOLMIN (1982) that *L. terrestris* developed a clitellum after about 3 months at 15 °C. MICHON (1954) measured duration times for the development of clitellum of 96 and 166 days at temperatures of 18 °C and 9 °C, respectively. These values are very close to those observed in the present experiments (tab. 5).
The age of maturing *L. terrestris* is temperature dependent. Development rates for animals with incipient clitellum growth (fig. 7) were fitted by a nonlinear function (equation (15)). The estimated parameters of this function are given in tab. 4. The development threshold \( T_{\text{min}} \) of *L. terrestris* lies close to 0 °C. TSUKAMOTO & WATANABE (1977) found for the compost inhabiting earthworm *Eisenia fetida* a development threshold of 5.6 °C. Maximum and optimum temperature for the development of *L. terrestris* are at 22.5 °C (tab. 4).

Temperature is not the only factor influencing age at maturation. HARTENSTEIN *et al.* (1979) showed that population density of the earthworm *E. fetida* influenced the amount of time needed for maturation. Nutrition may also be an important factor.

**Tab. 5**: Age in d of *Lumbricus terrestris* with incipient male pores and with incipient clitellum growth at different temperatures.

<table>
<thead>
<tr>
<th>°C</th>
<th>Food</th>
<th>Age with incipient male pores</th>
<th>Age with incipient clitellum growth</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.5</td>
<td>dandelion</td>
<td>180 (3.2)</td>
<td>213 (9.8)</td>
</tr>
<tr>
<td>10.0</td>
<td>dandelion</td>
<td>145 (16.4)</td>
<td>169 (18.4)</td>
</tr>
<tr>
<td>12.5</td>
<td>dandelion</td>
<td>118 (6.0)</td>
<td>135 (8.6)</td>
</tr>
<tr>
<td>16.0</td>
<td>dandelion</td>
<td>86 (12.8)</td>
<td>102 (15.0)</td>
</tr>
<tr>
<td>16.0</td>
<td>grass</td>
<td>91 (8.6)</td>
<td>112 (11.1)</td>
</tr>
<tr>
<td>17.5</td>
<td>dandelion</td>
<td>90 (30.8)</td>
<td>106 (33.9)</td>
</tr>
<tr>
<td>20.0</td>
<td>dandelion</td>
<td>66 (15.8)</td>
<td>82 (7.2)</td>
</tr>
<tr>
<td>22.5</td>
<td>dandelion</td>
<td>113 (55.2)</td>
<td>144 (54.4)</td>
</tr>
</tbody>
</table>

**Mortality**

There was no mortality up to rearing temperature of 17.5 °C before male pores appear. MICHON (1954), MEINHARDT (1974) and LOFS-HOLMIN (1982) reported similar results for *L. terrestris* between 9 and 18 °C. Thus, this species is most probably sensitive when changing stage, as is well known for other poikilotherms (CURRY & FELDMAN, 1987). At 25 °C, earthworms ceased to grow after 5 to 10 weeks. Body weight declined and all animals died before maturation began. It is not clear whether the observed mortality is temperature dependent or caused by the experimental system. It may be that high CO₂ concentrations developed in the rearing boxes or dietary factors have influenced the mortality, since the ventilation of the experimental boxes was not controlled and dandelion or grass was the only food.
Tab. 6: Percent mortality of *Lumbricus terrestris* during juvenile development up to incipient male pores and up to incipient clitellum growth at different temperatures in °C.

<table>
<thead>
<tr>
<th>°C</th>
<th>Food</th>
<th>Percent mortality with incipient growth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>male pores</td>
</tr>
<tr>
<td>7.5</td>
<td>dandelion</td>
<td>0</td>
</tr>
<tr>
<td>10.0</td>
<td>dandelion</td>
<td>0</td>
</tr>
<tr>
<td>12.5</td>
<td>dandelion</td>
<td>0</td>
</tr>
<tr>
<td>16.0</td>
<td>dandelion</td>
<td>0</td>
</tr>
<tr>
<td>16.0</td>
<td>grass</td>
<td>0</td>
</tr>
<tr>
<td>17.5</td>
<td>dandelion</td>
<td>0</td>
</tr>
<tr>
<td>20.0</td>
<td>dandelion</td>
<td>35</td>
</tr>
<tr>
<td>22.5</td>
<td>dandelion</td>
<td>65</td>
</tr>
<tr>
<td>25.0</td>
<td>dandelion</td>
<td>100</td>
</tr>
</tbody>
</table>
4.3 COCON PRODUCTION AND DEVELOPMENT

Reproduction of earthworms is influenced by a number of population characteristics (e.g. population density, biomass and age structure), as well as by external factors (e.g. soil temperature and moisture, and energy content of available food) (LEE, 1985). The species best studied with respect to reproduction is probably Eisenia fetida (Savigny) (GRAFF, 1974; TSUKAMOTO & WATANABE, 1977; HARTENSTEIN et al., 1979; REINECKE & KRIEL, 1981). The reproduction of other earthworm species has been investigated in the field or in pot experiments under seasonally varying temperatures by EVANS & GUILD (1948), PHILLIPSON & BOLTON (1977) and LAVELLE (1978), and at constant temperatures by NOWAK (1975), LOFS-HOLMIN (1982), CURRY & BOLGER (1984), BOSTRÖM (1988) and REINECKE & VILJOEN (1988). However, age and temperature dependency of the reproductive rate and the hatching success have not been studied to date except for E. fetida.

The incubation time of the cocoons depends on the temperature. This was shown for cocoons of Allolobophora chlorotica (Savigny) by GERARD (1960) and for cocoons of E. fetida by TSUKAMOTO & WATANABE (1977). For other earthworm species the incubation times were determined at varying (EVANS & GUILD, 1948) or at constant temperatures (MEINHARDT, 1974; NOWAK, 1975).

The aim of this study is to investigate the reproduction and cocoon incubation of Lumbricus terrestris, i.e. age and temperature dependent reproductive rates of the adults, the influence of the age of the adults and of the temperature on hatching success, and dry weight and incubation rate of cocoons.

4.3.1 Material and methods

Individuals of L. terrestris were collected from a meadow near the Swiss Federal Research Station for Farm Management and Agricultural Engineering in Tänikon using 0.005 % chloroacetophenone (CN) solution (chapter 5.1). The earth (clayey loam) used for the rearing originated from the lower part of the Aחר-horizon of the same meadow.

Reproduction and growth of adults

The earth for the rearing was dried slightly, crumbled by hand, sieved (5 mm mesh) and moistened to 40 % water content. Leaves of dandelion, collected in the Tänikon meadow, were used as food. They were dried for 3-4 h at 60 °C immediately after harvesting and then stored at 2 °C. Subadults of L. terrestris, collected in the field, were kept
in the laboratory at 15 °C until the clitellum fully developed at a body weight equal to about 1 g dry weight.

Cylindrical polyethylene boxes (diameter: 21 cm, height: 17 cm) with perforated lids were used for rearing the earthworms. Each box contained 1.6 kg (dry weight) soil, which had been firmed slightly. Two *L. terrestris* with fully developed clitellum were placed in each box and the cultures were then placed in constant temperature rooms at 10, 12.5 and 15 °C under continuous darkness. Four replicates were set up for each temperature treatment.

The earthworms were fed to excess with pieces of dandelion leaves (about 1 cm²), which were placed on the soil surface every week. At the beginning and thereafter every 4 weeks the soil was sorted by hand to collect the cocoons, except after 4 weeks at 10 and 15 °C. The adults were weighed, except at the beginning at 12.5 °C and after 4 weeks at 10 and 15 °C. The cocoons were cleaned carefully in tap water with a soft artists paintbrush and the adults were rinsed briefly in tap water. The live weight of the cocoons and of the earthworms was determined after blotting them with filter paper. If necessary, small amounts of tap water were added to the soil to maintain moisture content. The experiment was terminated after 56 weeks.

Some of the cocoons collected were damaged by handsorting. Thus, the dry weight of the cocoons produced by one adult pair in a time interval \( \Delta t \) was calculated by multiplying the total number of cocoons produced with the mean dry weight of the undamaged cocoons. The dry weight of the cocoons was calculated by transforming the live weights according to equation [19] (see below). Live weights of the adults were transformed into dry weights according to equation [13] (chapter 4.1). Rates of reproduction for *L. terrestris* were calculated with equation [17]:

\[
\Delta R = \frac{h \bar{V}}{\Delta t \left( W_{01} + W_{02} + W_{11} + W_{12} \right)^{0.5}} \tag{17}
\]

where

- \( \Delta R \): reproductive rate \([g \cdot g^{-1} \cdot wk^{-1}]\),
- \( h \): number of cocoons produced per adult pair in the time interval \( \Delta t \),
- \( \bar{V} \): mean dry weight \([g]\) of the cocoons produced in the time interval \( \Delta t \),
- \( W_{01}, W_{02} \): dry weight \([g]\) of the two adults at the beginning of a time interval \( \Delta t \),
- \( W_{11}, W_{12} \): dry weight \([g]\) of the two adults at the end of a time interval \( \Delta t \),
- \( \Delta t \): time interval \([wk]\).
The rates of reproduction, as a function of age, were fitted for each temperature with a model with two linear sections, one for increasing and another for decreasing reproductive rates (equation [18]):

$$\Delta R = a_1 A - a_2 (A - A_{\text{max}}) B$$

for $\Delta R \geq 0$  \[18\]

where

- $\Delta R$: reproductive rate [g g$^{-1}$ wk$^{-1}$],
- $a_1, a_2$: slopes of the regression lines,
- $A$: age [wk] of the adults,
- $A_{\text{max}}$: age [wk] of the adults, at which maximum reproduction occurs,
- $B$: boolean variable equal to 1 if $A > A_{\text{max}}$ and 0 otherwise.

The parameters of the regression equations were estimated by the method of least squares.

Survival of cocoons as a function of adult age and temperature

The cocoons produced were placed individually in jars (diameter: 2.5 cm, height: 1 cm). The bottom of the jars was covered by a 3-4 mm thick layer of plaster of Paris and water saturated to maintain humidity. The jars were controlled daily and the plaster of Paris remoistened periodically. They were kept in the dark except during the observations. Cocoons overgrown with fungi (hyphae) or bacteria were removed. Survival was calculated as the proportion of the incubated cocoons that hatched. A probit analysis (FINNEY, 1971; LINDER & BERCHTOLD, 1976) by the method of maximum likelihood was conducted for each temperature to describe the probits for the survival of the cocoons as a linear function of the age of the adults.

Development and weight of cocoons

Two batches of adult $L. \text{terrestris}$ were collected and reared at the conditions specified in tab. 13. Cylindrical polyethylene boxes with slightly compacted soil therein were used to keep the adults. They were covered with perforated lids. Food was added weekly on the soil surface so that nutrition was ad libitum. The cocoons were collected weekly by gently handsorting the soil, and carefully cleaned with a soft artists paintbrush in tap water.
<table>
<thead>
<tr>
<th>batch</th>
<th>°C</th>
<th>adults per box</th>
<th>soil per box in g dry weight</th>
<th>diameter in cm of the box</th>
<th>food</th>
<th>date of collection of adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>3</td>
<td>1600</td>
<td>21</td>
<td>mixture</td>
<td>autumn 87</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>2</td>
<td>800</td>
<td>10</td>
<td>dandelion</td>
<td>autumn 88</td>
</tr>
</tbody>
</table>

To find a dry weight / live weight relation, 22 cocoons from batch 2 were cleaned and weighed, dried at 105 °C for 20 h and then reweighed. A least square regression analysis with the model described in equation [19] was performed to describe dry weight as a function of the live weight:

\[
V = a_0 + a_1 V_l
\]  

[19]

where

- \( V \): dry weight [g] of cocoons,
- \( V_l \): live weight [g] of cocoons,
- \( a_0 \): intercept,
- \( a_1 \): slope.

Cocoons from both adult batches (n = 300) were placed individually in jars and reared as described above. The cocoons from batch 1 were used for incubations at 5, 7.5, 10, 12.5, 15, 20 and 25 °C. Those from batch 2 were first weighed and then incubated at 15, 17.5, 20, 22.5 and 25 °C. 25 cocoons were incubated per temperature. Freshly hatched juveniles were briefly rinsed in tap water, carefully blotted with filter paper and weighed. The remaining cocoons from batch 1 were opened after 24 months, those of batch 2 after 18 months.

The live weights of the incubated cocoons of batch 2 were transformed into dry weights by means of equation [19]. Equation [13] was used to calculate the dry weights of all hatched juveniles.

The relationship between the dry weights of cocoons and juveniles from batch 2 (n = 125) was described by equation [20]:

\[
V = a_0 + a_1 V_l
\]  

[20]
\[ W = a_0 + a_1 V \]  

where

- \( W \): dry weight [g] of hatchlings,
- \( V \): dry weight [g] of cocoons,
- \( a_0 \): intercept,
- \( a_1 \): slope.

A simple linear least square regression analysis was conducted to estimate the parameters of equation [20]. Incubation rates of the cocoons were calculated as the reciprocal of their incubation times. Survival was calculated as the proportion of the incubated cocoons that hatched.

### 4.3.2 Results and discussion

**Reproduction and growth of adults**

At about a dry weight of 1 g (fig. 8) the adults had a well developed clitellum and in most cases genital tumescences around some of the ventral pairs of setae were found between segments 24 - 26. These genital tumescences remained at the same place throughout the life of the adults and this character was used to identify the individuals in each box. The body weight of adults increased rapidly before reaching a plateau. A decrease in body weight after the reproductive period, as reported by MICHON (1954), was not observed. The maximum weight attained was highest at 12.5 °C (fig. 8). It may well be that *L. terrestris* reaches a maximum body weight at an optimum temperature.

The reproductive rate increased steeply to a maximum before decreasing slowly to zero with rising age (fig. 9). HARTENSTEIN *et al.* (1979) reported a similar skew shape of the age specific fecundity of *E. fetida* reared at different densities. The skewness may reflect the strategy of this animal to reproduce as quickly as possible after reaching sexual maturity. CSUZDI (1987) indicated for *Dendrobaena hortensis* (Michaelsen) that the distributions of the age specific fecundity of earthworms are not necessarily skewed. The parameters estimated for the model with two linear sections, one for increasing and another for decreasing reproductive rates (equation [18]), at different temperatures, are given in tab. 8. Maximum reproductive rates occurred after 6 to 16 weeks (tab. 8), depending on the temperature at which the adults were kept.

LOFS-HOLMIN (1982) reported for *L. terrestris* fed on semi-composted farmyard manure at 15 °C a fecundity of about 5.3 cocoons per adult pair per 4 weeks and CURRY & BOLGER (1984) estimated a maximum fecundity of slightly more than 4 cocoons per 4
weeks per adult pair reared with willow litter as food. The fecundities observed with
dandelion-fed adults (tab. 10) were at every temperature at nearly all age classes higher
than those reported by LOFS-HOLMIN (1982) and CURRY & BOLGER (1984). It is known
for other earthworm species that fecundity varies depending on food quality (EVANS &
GUILD, 1948). Therefore, the nutritive value of dandelion is assumed to be high.

The total biomass invested in reproduction ranged from 1.32 to 1.76 g dry weight per
adult pair (tab. 9). This is less than half of the biomass allocated to the growth of the
body. The total number of cocoons produced per adult pair was more than 100 (tab. 3).

Tab. 8: Parameter estimates of the piece wise regressions of the reproductive rates as a func­
tion of the age of the adult *Lumbricus terrestris* at different temperatures (equation [20]).
Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>°C</th>
<th>( a_1 )</th>
<th>( a_2 )</th>
<th>( A_{\text{max}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.0</td>
<td>0.0016 (0.00011)</td>
<td>0.0021 (0.00013)</td>
<td>15.7 (0.99)</td>
</tr>
<tr>
<td>12.5</td>
<td>0.0023 (0.00034)</td>
<td>0.0030 (0.00036)</td>
<td>13.1 (1.70)</td>
</tr>
<tr>
<td>15.0</td>
<td>0.0093 (0.00087)</td>
<td>0.0111 (0.00090)</td>
<td>6.2 (0.53)</td>
</tr>
</tbody>
</table>

Tab. 9: Cocoon biomass in g dry weight and cocoons produced by a pair of adult *Lumbricus terrestris* during their life (means and standard deviations).

<table>
<thead>
<tr>
<th>°C</th>
<th>total cocoon biomass per adult pair</th>
<th>total number of cocoons per adult pair</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.0</td>
<td>1.32 (0.182)</td>
<td>105.5 (15.11)</td>
</tr>
<tr>
<td>12.5</td>
<td>1.76 (0.514)</td>
<td>129.2 (36.23)</td>
</tr>
<tr>
<td>15.0</td>
<td>1.75 (0.308)</td>
<td>134.2 (22.62)</td>
</tr>
</tbody>
</table>

It is generally accepted that, in most species, only one juvenile successfully hatches
from each cocoon (LEE, 1985). However, the emergence of two (tab. 10), few times
three and once four juvenile *L. terrestris* from a single cocoon were observed.

The longevity of the adult stage of *L. terrestris* as reported by MICHON (1954) was
about 100 weeks at 9 °C and 106 weeks at 18 °C. Tab. 10 shows that at 15 and 12.5 °C
mean longevity was about 40 and 56 weeks, respectively. Therefore, it may be that the
completion time of the adult stage is shortest at about 15 °C and increases at lower and
higher temperatures.
Survival of cocoons as a function of adult age and temperature

Most of the cocoons changed their color from yellow to dark-brown in the course of their development. A few remained yellow and were suspected to be unfertilized. Some of the cocoons were visibly infested by fungi or bacteria during the experiment and the embryo therein died.

The survival of the cocoons was dependent on the age of the adults that produced them and on the temperature (fig. 10, tab. 11). Cocoons produced early in the reproductive period of an adult had a high probability of survival, whereas most of those from old adults failed to hatch.

Tab. 10: Cocoons and cocoons with twins that hatched per pair of adult *Lumbricus terrestris* (means and standard deviations) and survival of adults in the different age classes and at different temperatures.

<table>
<thead>
<tr>
<th>Age of the adults in wk</th>
<th>°C</th>
<th>Cocoons per adult pair</th>
<th>°C</th>
<th>Cocoons with twins per adult pair</th>
<th>°C</th>
<th>Surviving adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 8</td>
<td></td>
<td>7.5 (3.9)</td>
<td>9.3 (3.3)</td>
<td>29.0 (3.2)</td>
<td>.00 (0.00)</td>
<td>.75 (1.50)</td>
</tr>
<tr>
<td>8 - 12</td>
<td></td>
<td>10.3 (1.9)</td>
<td>10.8 (3.6)</td>
<td>25.8 (4.7)</td>
<td>.25 (0.50)</td>
<td>.50 (1.00)</td>
</tr>
<tr>
<td>12 - 16</td>
<td></td>
<td>9.8 (3.9)</td>
<td>17.0 (4.2)</td>
<td>20.8 (6.2)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>16 - 20</td>
<td></td>
<td>13.5 (2.1)</td>
<td>13.0 (3.6)</td>
<td>19.5 (6.4)</td>
<td>.75 (0.96)</td>
<td>.50 (1.00)</td>
</tr>
<tr>
<td>20 - 24</td>
<td></td>
<td>12.3 (2.2)</td>
<td>11.8 (2.8)</td>
<td>16.3 (3.4)</td>
<td>.50 (0.58)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>24 - 28</td>
<td></td>
<td>10.3 (1.9)</td>
<td>11.8 (4.9)</td>
<td>13.0 (4.1)</td>
<td>.00 (0.00)</td>
<td>.50 (1.00)</td>
</tr>
<tr>
<td>28 - 32</td>
<td></td>
<td>10.0 (2.5)</td>
<td>12.3 (5.1)</td>
<td>7.5 (7.3)</td>
<td>.25 (0.50)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>32 - 36</td>
<td></td>
<td>8.3 (2.6)</td>
<td>8.5 (6.6)</td>
<td>2.5 (5.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>36 - 40</td>
<td></td>
<td>9.0 (2.9)</td>
<td>10.8 (3.2)</td>
<td>0.0 (0.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>40 - 44</td>
<td></td>
<td>6.8 (1.9)</td>
<td>10.3 (5.1)</td>
<td>0.0 (0.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>44 - 48</td>
<td></td>
<td>6.0 (1.6)</td>
<td>10.5 (4.5)</td>
<td>0.0 (0.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>48 - 52</td>
<td></td>
<td>2.0 (2.2)</td>
<td>3.3 (5.3)</td>
<td>0.0 (0.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
<tr>
<td>52 - 56</td>
<td></td>
<td>1.0 (1.4)</td>
<td>0.3 (0.5)</td>
<td>0.0 (0.0)</td>
<td>.00 (0.00)</td>
<td>.00 (0.00)</td>
</tr>
</tbody>
</table>
Fig. 8: Age specific body dry weight of adult *Lumbricus terrestris* per week (wk) at different temperatures (means and standard deviations).

Fig. 9: Age specific reproduction (cocoon dry weight) per body dry weight of *Lumbricus terrestris* per week (wk) at different temperatures (means and standard deviations) (regression line parameters are estimated according to equation [20]).
Fig. 10: Survival of cocoons in relation to the age in week (wk) of adult *Lumbricus terrestris* that produced them at different temperatures (means and standard deviations). Solid lines are drawn based on the antiprobits of the theoretical survival according to the probit regression (tab. 11).

**Tab. 11:** Parameter estimates of the linear regressions of probits on the age of adult *Lumbricus terrestris* (a₁: intercept; a₂: slope). Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>°C</th>
<th>a₁</th>
<th>a₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.0</td>
<td>6.141</td>
<td>-0.041</td>
</tr>
<tr>
<td>12.5</td>
<td>6.260</td>
<td>-0.048</td>
</tr>
<tr>
<td>15.0</td>
<td>7.042</td>
<td>-0.099</td>
</tr>
</tbody>
</table>

**Weight and development of cocoons**

The dry weight of the cocoons was proportional to the live weight (fig. 11). The constant a₀ in equation [19] was eliminated from the regression model, since it is not significantly (p = 0.699) different from zero. The dry weight of the cocoons was 28.4% of their live weight (tab. 12). This is a higher proportion of the live weight than that observed for the juveniles (chapter 4.1). Therefore, developing embryos in the cocoons may need water. Water shortage due to dry soil conditions may be an important limiting factor for their development.

The dry weight of the hatchlings was linearly dependent on the dry weight of the cocoons (fig. 12). The constant a₀ was not eliminated from the regression model (equation
(20]), since it is different from zero with a probability $p = 0.060$. Parameters of the regression are given in tab. 12. It is assumed that the weight of a hatchling is proportional to the mass of the yolk in the cocoon, and that the envelope of the cocoon, which cannot be used as food by the developing embryo, accounts for the constant in the regression.

**Fig. 11**: Dry weight of the cocoons of *Lumbricus terrestris* as a function of their live weight.

**Fig. 12**: Dry weight of the hatchlings of *Lumbricus terrestris* as a function of the dry weight of cocoons.

**Fig. 13**: Developmental rates of the cocoons of *Lumbricus terrestris* per week (wk) at different temperatures (+ adults from batch 1, x adults from batch 2) (means and standard deviations).
The mean incubation time of the cocoons (tab. 13) incubated at low temperatures was longer than one year. A comparison with the observations of MEINHARDT (1974) at about 12 °C is difficult, since she ended her experiment after 32 weeks with only 75% of the cocoons hatched. The mode of the incubation times that she observed lies close to 13 weeks. This is much lower than the mean incubation times at comparable temperatures in this experiment. Maximum incubation rates (fig. 13) occurred at about 20 °C. At temperatures lower than 20 °C the incubation rate decreased rapidly and reached a plateau below 15 °C.

Tab. 12: Simple linear regression parameters of equation [19] and [20]. Standard errors are given in brackets.

<table>
<thead>
<tr>
<th>equation</th>
<th>(a_0)</th>
<th>(a_1)</th>
<th>(R^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>0.284</td>
<td>(0.0029)</td>
<td>0.998</td>
</tr>
<tr>
<td>5</td>
<td>-0.001</td>
<td>(0.0006)</td>
<td>0.744</td>
</tr>
</tbody>
</table>

Tab. 13: Incubation time in d, survival in % and dry weight in g of *Lumbricus terrestris* cocoons, and dry weight in g of hatchlings at different temperatures. Standard deviations are given in brackets.

<table>
<thead>
<tr>
<th>°C</th>
<th>adult batch</th>
<th>incubation time</th>
<th>survival</th>
<th>cocoon dry weight</th>
<th>hatchling dry weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>1</td>
<td>426 (74.9)</td>
<td>100</td>
<td>0.0083 (0.00131)</td>
<td></td>
</tr>
<tr>
<td>7.5</td>
<td>1</td>
<td>354 (49.1)</td>
<td>72</td>
<td>0.0085 (0.00127)</td>
<td></td>
</tr>
<tr>
<td>10.0</td>
<td>1</td>
<td>406 (128.5)</td>
<td>80</td>
<td>0.0082 (0.00102)</td>
<td></td>
</tr>
<tr>
<td>12.5</td>
<td>1</td>
<td>557 (135.8)</td>
<td>84</td>
<td>0.0064 (0.00240)</td>
<td></td>
</tr>
<tr>
<td>15.0</td>
<td>1</td>
<td>263 (113.9)</td>
<td>84</td>
<td>0.0078 (0.00154)</td>
<td></td>
</tr>
<tr>
<td>20.0</td>
<td>1</td>
<td>59 (7.8)</td>
<td>80</td>
<td>0.0082 (0.00142)</td>
<td></td>
</tr>
<tr>
<td>25.0</td>
<td>1</td>
<td>104 (2.1)</td>
<td>12</td>
<td>0.0084 (0.00113)</td>
<td></td>
</tr>
<tr>
<td>15.0</td>
<td>2</td>
<td>296 (110.1)</td>
<td>66</td>
<td>0.0147 (0.00192)</td>
<td>0.0096 (0.00141)</td>
</tr>
<tr>
<td>17.5</td>
<td>2</td>
<td>139 (81.4)</td>
<td>68</td>
<td>0.0134 (0.00157)</td>
<td>0.0086 (0.00132)</td>
</tr>
<tr>
<td>20.0</td>
<td>2</td>
<td>62 (12.6)</td>
<td>80</td>
<td>0.0136 (0.00194)</td>
<td>0.0091 (0.00165)</td>
</tr>
<tr>
<td>22.5</td>
<td>2</td>
<td>71 (30.5)</td>
<td>88</td>
<td>0.0147 (0.00163)</td>
<td>0.0102 (0.00124)</td>
</tr>
<tr>
<td>25.0</td>
<td>2</td>
<td>115 (39.4)</td>
<td>56</td>
<td>0.0139 (0.00194)</td>
<td>0.0083 (0.00170)</td>
</tr>
</tbody>
</table>
4.4 CONCLUSIONS

It was possible to investigate the whole life cycle of *Lumbricus terrestris* and the influence of the temperature on life cycle traits under optimum and controlled conditions with a relative simple experimental equipment. The equality of marginal conditions such as soil (-origin, -treatment and -storage), food (-origin, -treatment and -storage) and earthworm origin in the experiments of all three chapters is a feature of this study. The hypothesis that the temperature determines life cycle traits such as residence time in a particular stage or the growth rate was confirmed. At least for other litter feeding earthworm species such as *L. rubellus, L. castaneus* and *Dendrobaena* sp. information about the complete life cycle could be gained easily and in a short time with a similar equipment as used here. Since there is still a lack of information about the life cycles of many earthworms, studies filling this gap are supposed to be important.

The influence of environmental factors on the consumption is documented in chapter 4.1. The found relations may well provide a means for the understanding of the seasonal changes in litter disappearance rates in the field.

Low amounts of food available leads to an enhanced assimilation efficiency (chapter 4.1) as compared to conditions with food in excess. Thus, individuals probably optimize their gain in the spectrum of low food intake and high assimilation efficiency versus high food intake and low assimilation efficiency. A more complex situation is characteristic for the adults. They have to allocate the assimilates to processes such as maintenance, growth and reproduction and have to “decide” whether to use their time for digestion, food search at the surface or for mating at the surface. The optimization strategies developed by *L. terrestris* and other earthworm species to deal with suboptimum nutritional conditions or suboptimum time and their influence on the life cycle are not studied up to date. Since the conditions in the field are almost everytime suboptimum with respect to food available and time usable for food search and mating, behavioral studies in that domain would certainly shed light on important aspects of earthworm ecology.

Few supplementary experiments about the varying assimilation efficiency would complete this study on the life cycle of *L. terrestris*. Since the life cycle traits are described in a quantitative form, it will be easy to construct afterwards a conceptual simulation model of the population dynamics of *L. terrestris* based on quantitative life cycle traits.
5 POPULATION DYNAMICS OF LUMBRICUS TERRESTRIS L.

Population dynamics traditionally deal with the seasonal fluctuation of the abundance of populations as related to natality, mortality, immigration and emigration (e.g. KREBS, 1985; BEGON & MORTIMER, 1986). Further characteristics of a population are its distribution in age, weight and space. These distributions in conjunction with the prevailing environmental factors influence to an important extent the natality, mortality, immigration and emigration, and hence, the dynamic of the abundance. In several earthworm species diapause or quiescence may be additional factors that influence population dynamics.

Thus, the dynamics of populations are the result of diverse interrelated environmental and population factors. Since laboratory experiments about the life cycle of organisms never cover the whole spectrum of possible relations, complementary investigations on the population dynamics in the field are highly recommended to get a more precise image on the biology of an organism. This may be achieved by simple comparison of life cycle traits with the observed population dynamics in the field, or by constructing a life cycle based simulation model of the population dynamics and using the observed dynamics for a validation of the model.

The existing descriptions of the population dynamics of L. terrestris lasted for only about one year (LAKHANI & SATCHELL, 1970) or are based on pooled observations from a perennial meadow and an elm ash wood (NORDSTRÖM, 1976), and both did not account for the food available. Therefore, it is the aim of this work to redescribe the population dynamics of L. terrestris and to measure pertinent environmental conditions such as food available, soil water potential and soil temperature. Since extraction efficiency and spatial distribution of a population influence the reliability of the estimated abundances, these items are investigated in a foregoing study (chapter 5.1). The subsequent observed population dynamics of L. terrestris in a meadow are related to the life cycle traits of this animal measured in the laboratory (chapter 5.2).
5.1 Sampling

For earthworms several extraction techniques are known and have been described, e.g. in BOUCHÉ (1969), SATCHELL (1969), LEE (1985) and THIELEMANN (1986). Chemical solutions used as expellants require little time as compared with handsorting. The formaldehyde method, first published by RAW (1959), has been used by several authors (e.g. BOUCHÉ, 1969; SATCHELL, 1969; NORDSTRÖM & RUNDGREN, 1972; SPRINGETT, 1981; TERHIVUO, 1982; BAKER, 1985). It is well known that the efficiency of this method is subject to circadian (KRETZSCHMAR, 1982a; DANIEL, 1986) and seasonal (BOUCHÉ & GARDNER, 1984) changes. SATCHELL (1969), working with Lumbricus terrestris L., proposed a model for correcting seasonal changes, but the model was validated with only one sampling unit.

Inefficiencies in the extraction with expellants may be caused by toxic effects of the chemical (e.g. on motility) or by inadequate levels of exposition of the earthworms to the irritant substance. Thus, extraction efficiency of formaldehyde (which has toxic and irritant effects) was compared with chloroacetophenone which was assumed to only have irritant properties at the concentrations used. An adequate level of exposition had to be achieved through a better knowledge of the behavior of the earthworm populations.

The aim of this study is to investigate the efficiency of the chemical expellants formaldehyde or chloroacetophenone as compared to an application of chloroacetophenone followed by handsorting, and to test measures which might improve the exposition of L. terrestris to irritant substances. In addition, as investigations on the population dynamics were planned in the same plot, an approximate optimum sample size for the estimation of population densities of L. terrestris was determined.

5.1.1 Material and methods

Experiments

Location

Experiments were carried out in a nearly flat meadow area on a plot named “Chaiblen” near the Swiss Federal Research Station for Farm Management and Agricultural Engineering (FAT) in Tänikon (Canton of Thurgau, Switzerland). The meadow area of 1600 m² was divided into quadrants I, II, III, IV. The soil is reported to be a loamy, partially decarbonated, slightly pseudogleyic brown soil (ANONYMOUS, 1971). Parts of
the area, especially in quadrants II and IV, were filled several decades ago with stony soil. The area was turned into a meadow 15 years ago.

Treatments

As standard solutions, 40 % formaldehyde (formalin) and 10 % CN (chloroacetophenone) were used for the preparation of the expellants. For CN, dilutions were made not earlier than two hours before use. Metal box quadrats were used to delimit the treatment areas. They had a height of 10 cm and were pressed 2 - 3 cm into the soil. The borders of the metal box quadrats were heightened by 20 cm flexible plastic walls so as to hinder the earthworms from escaping. The treatment areas were 50 cm x 50 cm in treatments A to E and 100 cm x 100 cm in treatment F (tab. 14 and 2). The sampling units in treatment B to E were equal to the treatment areas. In treatment A and F the sampling units within the treatment areas were delimited by metal rings (diameter: 40 cm; height: 10 cm) and metal box quadrats of 50 cm x 50 cm, respectively. Five sampling units were considered for each quadrant and each treatment, and their position in the meadow area was determined by means of random numbers. Two experiments were organized:

Experiment 1 (tab. 14) was conducted to investigate the efficiency of the simple application of the chemical expellants formaldehyde and chloroacetophenone as compared to a chloroacetophenone application followed by handsorting. The treatment areas in treatments A and B were ponded for at least 40 min with CN. About 20 to 60 liters of the expellant per 0.25 m² were needed. Earthworms were collected during ponding and within 60 min thereafter. In treatment A the extraction by means of 0.008 % CN was followed by handsorting. For this purpose the soil beneath the sampling units was excavated by means of a borer of 40 cm diameter (0.126 m²) to a depth of 110 cm. Earthworms collected in treatment A (chloroacetophenone/handsorting) were pooled. In the treatments C and D the formaldehyde was applied as described by BOUCHÉ (1969).

Experiment 2 (tab. 15) was carried out to test measures that are considered to improve the exposition of the earthworms with the irritant substance and hence the extraction efficiency. The measures taken were a) daily repeated ponding of the treatment area, b) conduction of treatments after sunset, c) choice of treatment areas larger than the sampling units.

In treatment F the ponding was conducted on three subsequent evenings with CN solutions of 0.0002, 0.002 and 0.005 % on the first, second and third evening, respectively. Treatment E (tab. 15) was the same as treatment B in experiment 1 (tab. 1), but was carried out in November instead of June.
Tab. 14: Treatments used for expelling *Lumbricus terrestris* in experiment 1. (FA: formaldehyde, CN: chloroacetophenone).

<table>
<thead>
<tr>
<th>treatment</th>
<th>expel-</th>
<th>concen-</th>
<th>volume</th>
<th>treatment area</th>
<th>sampling area</th>
<th>day- time</th>
<th>date</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>CN</td>
<td>0.008%</td>
<td>ponded</td>
<td>1/4 m²</td>
<td>1/8 m²</td>
<td>16-19⁰⁰</td>
<td>17.06</td>
</tr>
<tr>
<td>B</td>
<td>CN</td>
<td>0.005%</td>
<td>ponded</td>
<td>1/4 m²</td>
<td>1/4 m²</td>
<td>16-19⁰⁰</td>
<td>19.06</td>
</tr>
<tr>
<td>C</td>
<td>FA</td>
<td>0.1%</td>
<td>2 x 5 l</td>
<td>1/4 m²</td>
<td>1/4 m²</td>
<td>08-10⁰⁰</td>
<td>10.06</td>
</tr>
<tr>
<td>D</td>
<td>FA</td>
<td>0.2%</td>
<td>2 x 5 l</td>
<td>1/4 m²</td>
<td>1/4 m²</td>
<td>17-19⁰⁰</td>
<td>10.06</td>
</tr>
</tbody>
</table>

* treatment A included a handsorting as specified in the text

Tab. 15: Treatments used for expelling *Lumbricus terrestris* in experiment 2. (CN: chloroacetophenone).

<table>
<thead>
<tr>
<th>treatment</th>
<th>expel-</th>
<th>concen-</th>
<th>volume</th>
<th>treatment area</th>
<th>sampling area</th>
<th>day- time</th>
<th>date</th>
</tr>
</thead>
<tbody>
<tr>
<td>E</td>
<td>CN</td>
<td>0.005%</td>
<td>ponded</td>
<td>1/4 m²</td>
<td>1/4 m²</td>
<td>16-19⁰⁰</td>
<td>07.11</td>
</tr>
<tr>
<td>F</td>
<td>CN</td>
<td>0.002%</td>
<td>ponded</td>
<td>1/4 m²</td>
<td>1/4 m²</td>
<td>17-22⁰⁰</td>
<td>04.11</td>
</tr>
<tr>
<td></td>
<td>CN</td>
<td>0.005%</td>
<td>ponded</td>
<td></td>
<td></td>
<td>17-22⁰⁰</td>
<td>05.11</td>
</tr>
<tr>
<td></td>
<td>CN</td>
<td>0.005%</td>
<td>ponded</td>
<td></td>
<td></td>
<td>17-22⁰⁰</td>
<td>06.11</td>
</tr>
</tbody>
</table>

Preservation and determination of the earthworms

Earthworms were killed and preserved using 4% formaldehyde. The preservative solution was renewed after one month.

Both *L. terrestris* and *L. castaneus* were present in the meadow area under investigation. *L. terrestris* with visible male pores were classified as adults. Small immatures were determined as *L. castaneus* if no pigmentation gradient was visible along the longitudinal axis.

Analysis of the experiments

Effects of treatments and quadrants

The level of significance was fixed for all statistical analyses to $\alpha = 0.05$. Earthworm numbers in treatment A (tab. 14) were multiplied by 2, because the sampling unit was only half of that in the other treatments. This seems to be justified, since preliminary
only half of that in the other treatments. This seems to be justified, since preliminary studies showed no influence of the size of the sampling unit on the proportion of the mean to the variance. Two-way analyses of variance (LINDER & BERCHTOLD, 1982; ZAR, 1984) with the data of treatments A through D with factors "treatment" and "quadrant" were conducted separately for adults and juveniles. Data used for the two-way analyses of variance were transformed according to equations [21] and [22] (ELLIOTT, 1977) for adults and juveniles, respectively:

\[ x^* = \sqrt{x} \]  \hspace{1cm} [21]

where

- \( x^* \): transformed value of \( x \),
- \( x \): number of adults per 0.25 m²,

and

\[ x^* = \sinh^{-1} \left( \sqrt{\frac{x + 0.375}{k - 0.750}} \right) \]  \hspace{1cm} [22]

where

- \( x^* \): transformed value of \( x \),
- \( x \): number of juveniles per 0.25 m²,
- \( k \): parameter of the negative binomial distribution (equation [23]).

It was hypothesized that in both experiments earthworm densities in the quadrants II+IV differed from those in the quadrants I+III due to the different soil quality, and that in experiment 1 treatment A was the most efficient treatment, B more efficient than C or D and C more efficient than D. These a priori hypotheses were tested in the two-way analyses of variance, if the effect of the quadrants or of the treatments was significant.

Frequency distribution

Data from experiment 1 (treatments B, C and D for adults and A, B, C, and D for juveniles) were used to test statistical distributions for their description. For the adults quadrants I + III and quadrants II + IV were analyzed separately. If mean and variance were not significantly different, it was tested whether a Poisson distribution would describe the data satisfactorily. Otherwise, a negative binomial distribution was evaluated. The significance of the differences between mean and variance as well as between measured and theoretical distributions was evaluated by Chi²-tests (ELLIOTT, 1977; LINDER & BERCHTOLD, 1979; ZAR, 1984). The parameter \( k \) of the negative
binomial distribution was iteratively estimated by the method of maximum likelihood according to equation [23] (LINDER & BERCHTOLD, 1979):

\[ \sum_{x=0}^{M} \frac{F_x}{k + x} = N \ln \left(1 + \frac{\bar{x}}{k}\right) \]  

where

- \( x \): frequency class,
- \( M \): number of frequency classes,
- \( F_x \): \( f_{x+1} + f_{x+2} + \ldots + f_M \),
- \( f_x \): observed frequency in class \( x \),
- \( N \): sum of all \( f_x \),
- \( \bar{x} \): mean density of juveniles per 0.25 m\(^2\),
- \( k \): parameter of the negative binomial distribution.

Sampling statistics

A stratified random sample with proportional allocation, but where the strata are ignored for the calculation of the variance, does resemble a simple random sample with respect to the variance (COCHRAN, 1977). Furthermore, the gain in precision due to stratification (design effect) is assumed not to be important with few strata and only small differences between the strata. Therefore, for the sake of simplicity approximate estimations of the optimum sample size for a desired precision were calculated on the assumption of a random sampling.

Reliability (\( C \) in equation [24] and [25]) represents a defined ratio between standard error and the mean. This criterion is commonly used in research work, while in decision making it is more frequent to express the reliability in terms of probabilistic statements (RUESINK, 1980). The optimum sample size for estimating population densities was calculated according to equation [24] for Poisson distributed data and according to equation [25] for negative binomial distributed data, as suggested by KARANDINOS (1976):

\[ n = \frac{1}{\bar{x} \cdot C^2} \]  

where

- \( n \): sample size,
- \( C \): coefficient of standard error as a fraction of the mean,
- \( \bar{x} \): mean density of the adults,
and

\[
\frac{1}{\bar{x}} + \frac{1}{k} = \frac{1}{nC^2}
\]

where

- \( n \): sample size,
- \( C \): coefficient of standard error as a fraction of the mean,
- \( \bar{x} \): mean density of the adults,
- \( k \): parameter of the negative binomial distribution.

### 5.1.1 Results and discussion

Effects of treatments and quadrants

Treatment A (CN and handsorting) was the most efficient extraction method for the adults (tab.16). No difference was found for the adults between the density estimates accomplished by treatments B (CN), C (formaldehyde) and D (formaldehyde) (tab. 16). The results show that CN was not superior to formaldehyde. In experiment 2 the adults were extracted more efficiently by treatment F than by treatment E (tab. 5). Therefore, it is assumed that measures which improve the exposition of the earthworms to the irritant substance enhance the efficiency of the extraction. For juveniles the choice of treatment had no influence on the efficiency of the extraction in both experiments (tab. 17 and tab. 19). The extraction efficiency in treatment A is supposed to be close to 100 % for both adults and juveniles.

In the Tänikon meadow adults of *L. terrestris* build deep burrows of about 90 cm depth, whereas juveniles live closer to the surface. The burrows of adults are large macropores which bypass capillary flow through the soil matrix (BEVEN & GERMANN, 1982) and are rapidly filled with liquids. There are two factors that possibly prevent the expellant from completely filling the burrows of the adults. Firstly, the enclosure of the burrows by the earthworms, as is observed frequently in dry seasons. Secondly, air trapped between the penetrating expellant and air impervious soil layers, keeping the solution to get into contact with the earthworms. FLÜHLER et al. (1986) mentioned discrete entrapped air volumes in the soil of a few microliters to more than 1000 liters and air pressures ranging to 3 kPa above atmospheric pressure after flood irrigation.

*L. terrestris* has circadian depth preferences and is near the surface at night (JOYNER & HARMON, 1961). Since the air is not expected to be entrapped near the surface, the extraction efficiency with expellants should be better at night than during day time. The
*L. terrestris* a higher extraction efficiency at night than at day with the formaldehyde method.

An amelioration of the efficiency of chloroacetophenone was only achieved through very time consuming measures that probably improved the exposition to the irritant chemical. The electrical method of THIELEMANN (1986) is also time consuming and too little is known about its efficiency, especially for deep burrowing earthworms. Handsorting may be the most efficient earthworm extraction method, but requires by far the greatest amount of time. The choice of an adequate extraction technique remains difficult and is determined by the aims of the study and by variables such as soil type, soil depth and earthworm species (LEE, 1985).

In summer and autumn 1986 the density of the adults was higher in the quadrants I+III than in the quadrants II+IV (tab. 16 and 5). This may be due to different soil properties in the quadrants, since several decades ago parts of the area of quadrants II and IV have been filled with stony soil.

The density of the juveniles did not differ between quadrants in the summer (tab. 17), but in autumn 1986 juveniles were more abundant in the quadrants I+III than in the quadrants II+IV (tab. 19).

---

Tab. 16: Two-way analysis of variance with treatments A to D in the quadrants I to IV for adults of *Lumbricus terrestris*.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>79</td>
<td>39.198</td>
<td>0.496</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrants</td>
<td>3</td>
<td>4.381</td>
<td>1.460</td>
<td>4.161</td>
<td>0.009</td>
</tr>
<tr>
<td>I+III vs. II+IV</td>
<td>1</td>
<td>4.227</td>
<td>4.227</td>
<td>12.044</td>
<td>0.001</td>
</tr>
<tr>
<td>Treatments</td>
<td>3</td>
<td>3.430</td>
<td>1.143</td>
<td>3.258</td>
<td>0.027</td>
</tr>
<tr>
<td>A vs. B+C+D</td>
<td>1</td>
<td>2.752</td>
<td>2.752</td>
<td>0.842</td>
<td>0.007</td>
</tr>
<tr>
<td>B vs. C+D</td>
<td>1</td>
<td>0.392</td>
<td>0.392</td>
<td>1.116</td>
<td>0.295</td>
</tr>
<tr>
<td>C vs. D</td>
<td>1</td>
<td>0.286</td>
<td>0.286</td>
<td>0.816</td>
<td>0.370</td>
</tr>
<tr>
<td>Interactions</td>
<td>9</td>
<td>1.525</td>
<td>0.169</td>
<td>0.483</td>
<td>0.881</td>
</tr>
<tr>
<td>Rest</td>
<td>64</td>
<td>22.462</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Tab. 17: Two-way analysis of variance with treatments A to D in the quadrants I to IV for juveniles of *Lumbricus terrestris*.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>79</td>
<td>3.004</td>
<td>0.038</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrants</td>
<td>3</td>
<td>0.165</td>
<td>0.055</td>
<td>1.335</td>
<td>0.271</td>
</tr>
<tr>
<td>Treatments</td>
<td>3</td>
<td>0.053</td>
<td>0.018</td>
<td>0.429</td>
<td>0.733</td>
</tr>
<tr>
<td>Interactions</td>
<td>9</td>
<td>0.144</td>
<td>0.016</td>
<td>0.389</td>
<td>0.936</td>
</tr>
<tr>
<td>Rest</td>
<td>64</td>
<td>2.642</td>
<td>0.041</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tab. 18: Two-way analysis of variance with treatments E and F in the quadrants I to IV for adults of *Lumbricus terrestris*.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>39</td>
<td>14.270</td>
<td>0.366</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrants</td>
<td>3</td>
<td>2.502</td>
<td>0.834</td>
<td>2.948</td>
<td>0.048</td>
</tr>
<tr>
<td>I+III vs. II+IV</td>
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<td>0.530</td>
<td>0.530</td>
<td>1.872</td>
<td>0.181</td>
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<tr>
<td>Treatments</td>
<td>1</td>
<td>1.131</td>
<td>1.131</td>
<td>3.998</td>
<td>0.054</td>
</tr>
<tr>
<td>Interactions</td>
<td>3</td>
<td>1.052</td>
<td>0.351</td>
<td>1.239</td>
<td>0.312</td>
</tr>
<tr>
<td>Rest</td>
<td>32</td>
<td>9.055</td>
<td>0.283</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tab. 19: Two-way analysis of variance with treatments E and F in the quadrants I to IV for juveniles of *Lumbricus terrestris*.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>39</td>
<td>2.469</td>
<td>0.063</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quadrants</td>
<td>3</td>
<td>0.598</td>
<td>0.199</td>
<td>4.763</td>
<td>0.007</td>
</tr>
<tr>
<td>I+III vs. II+IV</td>
<td>1</td>
<td>0.400</td>
<td>0.400</td>
<td>9.554</td>
<td>0.004</td>
</tr>
<tr>
<td>Treatments</td>
<td>1</td>
<td>0.053</td>
<td>0.053</td>
<td>1.259</td>
<td>0.270</td>
</tr>
<tr>
<td>Interactions</td>
<td>3</td>
<td>0.078</td>
<td>0.026</td>
<td>0.624</td>
<td>0.605</td>
</tr>
<tr>
<td>Rest</td>
<td>32</td>
<td>1.340</td>
<td>0.042</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Tab. 20: Densities per 0.25 m² of *Lumbricus terrestris* estimated with treatments A to F in the area covered by quadrants I + III, and II + IV, respectively (Means and standard deviations).

| treatment | adults | | juveniles | | | 
|---|---|---|---|---|---|--- |
| | quadrants I+III | quadrants II+IV | quadrants I+III | quadrants II+IV | | 
| A | 8.6 (3.53) | 6.4 (3.37) | 19.0 (6.05) | 20.0 (9.29) | | 
| B | 6.3 (2.50) | 5.0 (1.33) | 18.6 (8.90) | 16.5 (8.19) | | 
| C | 6.7 (3.09) | 4.3 (2.41) | 20.2 (7.94) | 18.8 (7.98) | | 
| D | 5.9 (1.91) | 3.5 (2.41) | 18.9 (6.31) | 17.5 (7.85) | | 
| E | 7.8 (3.49) | 8.4 (3.27) | 20.7 (7.82) | 14.6 (4.65) | | 
| F | 11.9 (3.78) | 8.5 (3.34) | 20.0 (5.08) | 19.0 (7.59) | | 

Frequency distributions

The estimated means did not differ significantly from variances (Chi², p > 0.999) for juveniles and adults. The data on the adults in both quadrants I + III and quadrants II + IV could be described by Poisson distributions (Chi², p > 0.999).

A negative binomial distribution was chosen for the description of the data of juveniles, because the observed juvenile distribution differed significantly from a Poisson distribution (Chi², p < 0.001). The parameter k of the negative binomial distribution was estimated to be 6.1998. A Chi²-test revealed no significant differences (p > 0.999) between observed and theoretical negative-binomially distributed values.

Thus, juveniles are probably more contagiously distributed than adults. To make further inferences from frequency distributions on the spatial distribution of *L. terrestris* is delicate, since the perceived distribution pattern may depend on the sample unit size (WILSON *et al.*, 1989).

Sampling statistics

Optimum sample size is density dependent (fig. 15 and 2) for both adults and juveniles. For a juvenile density of 20 individuals per 0.25 m², which is about that observed in the Tänikon meadow, according to equation [25] a sample size of 6 is enough to reach a desired reliability of C = 0.2. The adults were less abundant than the juveniles (tab. 7). Their optimum sample size equals 5 according to equation [24], assuming a density of 6 individuals per 0.25 m² and C = 0.2. Thus, density estimations with a reliability C = 0.2 may be carried out with little sampling effort. Of course population density fluctuates with time and this has to be taken into account for planning samplings. For further investigations a sample size of 10 was considered to allow reliable estimates even if the densities fall to about one half for adults and one quarter for juveniles of those reported here.
Only in few earthworm habitats such as meadows or some deciduous forests the density of juveniles and adults may be high enough to allow reliable (C = 0.2) estimates with low sampling effort. Many other habitats have lower population densities or are less homogeneous than that in this study. There, a stratification might be a prerequisite for reliable estimates of the population density. Sample sizes leading to reliabilities of C = 0.05 as recommended by SOUTHWOOD (1978) or of C = 0.10 as exemplified in fig. 15 and fig. 16 will be taken in field studies on earthworms rarely, since destructive extraction methods such as handsorting, formaldehyde and chloroacetophenone application, or electrical extraction methods are too time consuming. Therefore, attempts to ameliorate sampling methods for earthworms should not only concentrate on how to improve or control the extraction efficiency, but also should focus to reduce the time needed for the sampling.
5.2 POPULATION DYNAMICS IN A MEADOW

The dynamics of populations is generally induced by fluctuating environmental factors such as temperature, soil moisture and the amount and quality of food available. These factors influence life cycle traits such as body weight, age at the onset of maturity, reproduction, longevity, and incubation time of cocoons. Information on life cycle traits is necessary for an understanding of observed population dynamics and for the construction of simulation models. LAVELLE and MAYER (1977) included in their model "Allez-les-vers" several life cycle traits and could satisfactorily simulate the population dynamics of the grass savanna inhabitant earthworm *Millsonia anomala*. Others interpreted observed population dynamics of earthworms more (GERARD, 1967; LAKANI & SATCHELL, 1970; SOLBE, 1971 and NOWAK, 1975) or less (EVANS & GUILD, 1947; RHEE & NATHANS, 1973, NORDSTRÖM, 1976; PHILLIPSON *et al.*, 1978, RÖMBKE, 1987 and ROZEN, 1988) in relation to the animals life cycle traits.

Recent investigations in the laboratory (chapters 4.1, 4.2 and 4.3) elucidated before unknown life cycle traits of *Lumbricus terrestris* at controlled environmental conditions. To compare these findings with life cycle traits in the field, the population dynamics in a meadow was investigated during two seasons. Periodical observations were made on the abundance and the body dry weight distributions of *L. terrestris* and pertinent environmental factors such as soil temperature, soil water potential and the amount of food available.

5.2.1 Material and methods

Location

The location is a meadow area on a plot named "Chaiblen" near the Swiss Federal Research Station for Farm Management and Agricultural Engineering (FAT) in Tänikon (Canton of Thurgau, Switzerland). This meadow area is nearly flat. The soil is reported to be a loamy, partially decarbonated, slightly pseudogleyic brown earth (ANONYMOUS, 1971). The plot was turned into a meadow 15 years ago. The investigations were carried out in two quadrants of 20 m x 20 m having one side in common, and named quadrant I and III in chapter 5.1.
Soil water potential

Tensiometers were installed in the center of each of the two quadrants. They were positioned as described by VOGELSANGER (1986) to depths of 15, 30 and 60 cm. There were 3 tensiometers in each depth in both quadrants. Soil water potential readings were accomplished in the vegetation period every one to three weeks by a pressure transducer (MARTHALER et al., 1983).

Soil temperature and precipitations

Soil temperatures at a depth of 5 and 50 cm and precipitations were measured by an automatic weather recording station of the Swiss Meteorological Institute. The automatic station was about 30 m alongside of the meadow area under investigation. Based on the measured data, mean weekly soil temperatures and total weekly precipitations were calculated.

Vegetation

The vegetation was cut by means of a lawn-mower every one to three weeks during the growing season. Thus, the cut plant material was available as food to the surface feeding earthworm species.

Ten (5 per quadrant) sampling units of the cut plants, whose coordinates have been determined by random numbers, were taken immediately after the mowing. The sampling unit was 1/16 m². The plant material was collected with a small vacuum cleaner and dried at 105 °C for 24 h.

Sampling

The sampling of earthworm populations was conducted from April 1987 to September 1988. The coordinates of the sampling units were determined by means of random numbers. Quadratic iron frames (50 cm x 50 cm) were used to delimit the sampling units. They had a height of 10 cm and were pressed 2 - 3 cm into the soil. The borders of the frames were heightened by 20 cm flexible plastic walls so as to hinder the earthworms from escaping.

For L. terrestris, the extraction by means of formaldehyde or chloroacetophenone solutions is equally efficient for juveniles and almost equally efficient for adults as is the extraction by handsorting (chapter 5.1). Thus, the abundance of this species is reliably estimated with a sample size appropriate to the variability and the density of the population.
In the first year the earthworms were extracted by means of cloroacetophenone, which was applied in four subsequent evenings to each sampling unit. The concentrations used were 0.0002, 0.002, 0.005 and 0.01 %. Both sampling units and the treated area were 0.25 m². Five sampling units were taken from each quadrant. In 1987 5 samples (total 50 sampling units) were taken and spaced by about 2 months.

The main goal in the second year was to follow the dynamics of the juveniles. Therefore, to reduce the input of labour, the earthworms were extracted by means of about 30 l formaldehyde (0.2 %) per 0.25 m², except at April 11, June 20 and September 19, when cloroacetophenone was used as in the previous year. In samplings by means of formaldehyde only 6 sampling units (3 per quadrant) were taken per sample. In 1988 a total of 9 samples (total 66 sampling units) were taken.

Preservation and determination of the earthworms

The earthworms were killed and preserved using 4 % formaldehyde. The preservative solution was renewed after one month. The identification of the earthworms and the weighings were conducted in summer 1989. Both *L. terrestris* and *L. castaneus* were present in the meadow. Small immatures of *Lumbricus* sp. were determined as *L. castaneus* if no pigmentation gradient was visible dorsally along the longitudinal axis. Those individuals with visible male pores but without a clitellum projecting over the body were classified as subadults.

**Body weight of *L. terrestris***

The preserved *L. terrestris* were rinsed in tap water, blotted with filter paper and weighed. Assuming a weight loss due to the preservation of 9.5 % of the live weight (CUENDET, 1985) and that live weight corresponds to that of *L. terrestris* acclimatized to 10 °C, the dry weight / live weight relation from chapter 4.1 was modified to account for the preserved weight (equation [26]):

\[
W = \frac{W_l}{0.905 \times 0.1926} \tag{26}
\]

where

\[W: \text{ dry weight [g]},\]
\[W_l: \text{ preserved weight [g]}.\]

To follow the growth of weight cohorts, frequencies per body dry weight category per 0.25 m² were calculated. Body dry weight categories were spaced by 0.03 g intervals.
5.2.2 Results and discussion

Environmental factors

The soil water potential never reached low values during the investigation period (fig. 16). In summer 1987 some rare superficial fissures were observed in the loamy soil. Because the precipitations occurred regularly throughout the two years (fig. 17), the soil dried out only at the surface for short periods.

The mean weekly soil temperatures in January, February, May and June were in 1987 a few °C lower than in 1988 (fig. 18). In both years the mean weekly soil temperature in a depth of 5 cm increased not steeper and not higher than in a depth of 50 cm. This is presumably caused by heat losses due to water evaporation. During autumn and winter the soil was colder at a depth of 5 cm than at 50 cm. In the winter 1987 mean weekly soil temperatures below -5 °C were observed.

In 1988 more plant material was mowed than in 1987 (fig. 19). This may reflect different productivities of the meadow in the two years. Possible reasons are firstly environmental factors such as different temperatures and soil water potentials and secondly a fertilization due to the plant material incorporated into the soil by the earthworms during the first year.

The dry weight of the monocotyledones was 60 - 90 % of the total dry weight of mowed plants. In 1987 about 5 % of the dicotyledones was clover; in 1988 no more clover was observed and mosses had a higher abundance in the meadow.

Fig. 16: Soil water potentials interpolated by the method of distance weighed least squares for different soil depths in the Tänikon meadow during 1987 and 1988.
Fig. 17: Weekly precipitation in mm recorded by an automatic weather recording station in Tänikon in 1987 and 1988.

Fig. 18: Weekly soil temperatures (means) at soil depths of 5 cm (solid line) and 50 cm (pointed line) during 1987 and 1988 recorded by an automatic weather recording station in Tänikon.

Fig. 19: Mowed plant material (cumulative dry weight) per 0.25 m² in the Tänikon meadow in 1987 and 1988.
Lumbricid species complex

Following lumbricid species were found in the meadow in addition to *L. terrestris*: *Allolobophora chlorotica* (Savigny), *Aporrectodea rosea* (Savigny), *A. icterica* (Savigny), *A. longa* (Ude), *A. caliginosa* (Savigny), *Octolasion cyaneum* (Savigny), *O. lacteum* (Orley), *Eiseniella tetraedra* (Savigny) and *L. castaneus*.

The method used for earthworm extraction has the disadvantage that most species other than *L. terrestris* are not efficiently expelled (Lee, 1985). Hence, the study was confined to this species.

Population dynamics of *L. terrestris*

According to equation [26] the preserved weight (4% formaldehyde) was equal to the dry weight multiplied by 4.699. This value is lower than that determined by Lakhani & Satchell (1970). The difference may be due to the short (4 days) preservation time used by these authors.

The adults of *L. terrestris* had a rather constant abundance during the two years of investigations (fig. 20). The dry weight of individuals ranged from about 0.3 to 1.3 g. Lakhani & Satchell (1970) collected *L. terrestris* with slightly higher body dry weights, but only few individuals weighed more than 1.4 g (Merlewood) and 1.6 g (Heaning Wood). Body dry weights near 2 g, as observed in laboratory experiments (chapter 4.3), were not observed in the field.

Subadults had body dry weights often as high as those of the adults (fig. 21 and 22). Only in November 87, March 88 and April 88 the body dry weight of the subadults was lighter and about 0.6 g. Laboratory experiments (chapter 4.2) suggest that subadults should have mean body dry weights below 0.75 g. Since body dry weights of the subadults in the field were often heavier, particularly on September 19, 1988, it is assumed that *L. terrestris* is capable to delay the maturation.

The density of the juveniles increased in both years in spring and autumn, but decreased in summer and winter (fig. 20). In the winter the abundance of juveniles dropped slightly down to about two third of that in autumn. Increasing juvenile densities (fig. 20) were related to high frequencies in the lowest body dry weight category (fig. 21 and 22). It is assumed that this was mainly caused by juveniles hatching from cocoons and that animals entering the lowest weight category by losing weight play a minor role. According to tab. 13 in chapter 4.3 the mean incubation time of cocoons at 15, 17.5 and 20 °C is 279, 139 and 61 days, respectively. The cocoons of *L. terrestris* are mainly deposited in soil depths less than 30 cm (Gerard, 1967). Since the soil temperatures at depths of 5 and 50 cm were close to 17.5 °C during about 3 months in the summer (fig. 18), it is
probable that the cocoons hatching in the autumn were produced in the spring. In the spring the frequencies in the lightest weight category of juveniles were lower than in the autumn, suggesting that hatching in the spring was less numerous. Low soil temperature leads to very low nutritional requirements and a low growth rate (chapters 4.1 and 4.2) of *L. terrestris*. Since the mean weekly soil temperatures between December and March were below 5 °C (fig. 18), it is expected that individuals keep about the same weight through that period of time. The decrease in the abundance of juveniles may be caused by mortalities induced by short freezing periods near the soil surface or by predation.

The juvenile cohort with the mode at 0.09 g in July 27, 1987 grew until November of the same year to a dry weight of about 0.2 g (fig. 21) and reached probably the subadult stage in September 1988 (fig. 22). Hatchlings from autumn 1987 (fig. 21) grew predominantly in the next year and had after nearly one year a body dry weight below 0.3 g (fig. 22). This is quite surprising since it was demonstrated that hatchlings became adult at unlimited conditions in the laboratory at a much shorter time (chapter 4.2).

*L. terrestris* (adults and juveniles) feed mainly on dead leaves, with roots as minor component of the diet (BOUCHE & KRETZSCHMAR, 1974; FERRIERE, 1980). Therefore, the amount of mowed plant material left on the soil surface is a good measure for the potential food available for *L. terrestris*. Assuming that the cumulative amount of cut plants in fig. 19 is linear, about 5 and 8 g food per 0.25 m² per week were potentially available to *L. terrestris* in 1987 and 1988, respectively. Considering that other organisms (e.g. microorganisms, other earthworm species, snails) also fed on the same food, even less was probably at the disposition of *L. terrestris*. The food quantity needed by *L. terrestris* under optimum laboratory conditions (food *ad libitum*, no soil water constraints) can be calculated for a specified temperature with a nonlinear equation which was determined in chapter 4.1. This equation was obtained from experiments with dandelion, but it was demonstrated that grass is eaten in similar amounts. As an example, the biomass of *L. terrestris* per 0.25 m² on May 30, 1988 was calculated to be 19.2 g in the Tänikon meadow. At 15 °C this biomass requires theoretically about 23.3 g, at 20 °C about 42.1 g food per week. Since such food quantities were never available in the Tänikon meadow, individuals of *L. terrestris* had to face intense intraspecific competition for food resources. NIELSEN & HOLE (1964) observed in the field that *L. terrestris* line the upper 10 cm of their burrows with leaves. In own laboratory experiments *L. terrestris* quite frequently pulled considerable amounts of grass in their burrow and leave it there without immediately ingesting it. Since food pulled into the burrow is no more available for other earthworms, this behavior is certainly a competitive strategy to gain more food than others. It is assumed that shortage in food is the main reason why in the field juveniles grow slower, the weight of adults is lighter and maturation occurs at heavier body dry weights than under laboratory conditions.
The stability of the adult density and the indicated intraspecific resource competition are arguments which confirm the view of SATCHELL (1980) that *L. terrestris* is more 'K'-selected than other members of the *Lumbricidae*. This study improved the understanding of the population ecology of *L. terrestris* through the comparison of life cycle traits observed in the laboratory with the population dynamics in the field. In further investigations a much closer view on processes regulating the population dynamics in the field should be attained through the construction of life cycle trait based models of the population dynamics.

**Fig. 20:** Abundance per 0.25 m² of *Lumbricus terrestris* during 1987 and 1988 in a meadow in Tänikon (•: adults; solid line: subadults; ◦: juveniles).
Fig. 21: Frequencies (number per dry weight category per 0.25 m²) of juvenile, subadult and adult *Lumbricus terrestris* during 1987 in a meadow in Tänikon.
Fig. 22: Frequencies (number per dry weight category per 0.25 m²) of juvenile, subadult and adult *Lumbricus terrestris* during 1988 in a meadow in Tänikon.
5.3 CONCLUSIONS

The soil is almost always a heterogeneous 3-phase matrix (solid, gas, liquid) with a composition varying over time and space. Thus, it is difficult to predict or control the temporal and spatial dispersion in the soil of irritants such as formaldehyde, chloroacetophenone or electric current. Further investments in the study of the extraction of earthworms by chemical solutions seem not justified because of possible toxic side effects of these methods. More promising for the future is the extraction of earthworms by low voltage electricity as described by THIELEMAN (1986). However, this method should be improved towards a reliable and time-saving technique. Indeed, further investigations should not concentrate only to improve or to control the extraction efficiency, but should focus to reduce the time needed for the sampling as well. The indicated dependency of the sample size on the earthworm density and distribution well supports the need of such a method for studies in inhomogeneous ecosystems with low earthworm densities.

The study of the population dynamics in the field did reveal results complementary to the laboratory experiments. The importance of resource competition was only obvious after a comparison between the food available in the meadow with that calculated to be needed by the *L. terrestris* population on the base of the laboratory experiments.

In the laboratory experiment temperature dependent mortality of juveniles occured when changing stages. Nevertheless, in the meadow the density of juveniles dropped before reaching the subadult or adult stage. This phenomenon may be explained either by migration or mortality. Since food was in shortage, starvation was probably an important mortality factor, but other factors such as predation and parasitism may have been important as well. It would be astonishing rather, if such a high quantity and quality biomass was not exploited by several predators. Indeed, e.g. badgers in NW Europe feed predominantly on earthworms, especially *L. terrestris* (KRUUK, 1986). Other predators are mentioned in MACDONALD (1983).

Adults in the laboratory produced cocoons constantly during their reproductive phase. However, in the meadow the hatching of juveniles from the cocoons occurred in limited periods of time in spring and autumn. The "synchronization" of the hatching in the meadow may be the consequence of an intermittent reproductive activity of the adults. Nevertheless, in spring a cocoon development which is fast only at high temperatures (20 °C) may be the main reason for the observed synchronization.

Other questions with respect to the ecological strategies of earthworms (behavior, life history strategy, population regulation) may arise if one compares laboratory and field studies. A much closer link between the results of the life cycle studies and the population dynamics would be achieved through the construction of a simulation model of the popu-
lation dynamics of *L. terrestris*. The detailed results in the first chapter of this thesis invoke the impression that it would be a rather forward task. However, such a model could be built only on several assumptions with regard to e.g. the age structure of the population at the beginning, the relevant soil temperature for this circadian up and down moving animal, and the food, which is not necessarily composed of dead superficial plant material only. Therefore, a model would certainly invoke as many questions as it could answer and should be designed properly for the solution of specific questions.

In an advanced stage a simulation model would also allow to relate soil processes to the abundance and activity of the earthworms. Further studies on the influence of environmental factors and body weight or age on characteristics such as the depth and diameter of the constructed burrows, the amount of soil ingested together with organic material and the activation of the microflora in the casts through gut passage should be performed. Integrating the results of such studies in a simulation model would allow to make statements about complex soil biological processes that are important for the maintenance of soil fertility.
6 REFERENCES


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CURRICULUM VITAE

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