gained on quite different soils. Is there any way that we can approach the problem more rationally? I suggest there is: Let us first construct a modal soil from the point of view of the pasture ecosystem and then see how we might modify our present soils to approach this ideal.

The prairie soils may be considered the ideal for the brown-grey and yellow-grey earth zone, and the brown forest soil for the yellow-brown earth zone. If we could modify soil processes so that they were directed towards these ideals we would also modify the whole ecosystem. For example, increasing the base status of subsoils as well as topsoils would create conditions more favourable to soil flora and fauna which in turn would improve structure, aeration, water storage capacity and drainage, as well as increase the depth of soil available for grass roots. It would be necessary for ecologists to take an active part in any study of soil amelioration because the kinds of plants growing on the soil and the way they are utilised will influence the changes taking place. The piecemeal study of parts of the pasture ecosystem such as plant breeding and soil chemistry have their place, but there is also need for a broader approach—a pedological-ecological one which would integrate these individual studies into the whole system.

THE EFFECT OF EARTHWORMS ON PASTURES

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INTRODUCTION

Without earthworms pasture production may be limited to slightly more than half the true potential. With beneficial earthworms increased production is associated with pronounced physical changes that are readily observed in the field. Changes in both physical and chemical properties are revealed by analyses of soils from pastures with and without beneficial earthworms. Some of these changes are direct results of earthworm activity, others may be brought about indirectly.

BENEFICIAL SPECIES

Lee (1959) has recognised 192 species in New Zealand. The great majority are natives found mainly under native vegetation. Some are, however, found under sown pastures. Populations as high as 20 per square foot have been recorded in the absence of introduced species with no obvious beneficial effects.

Of the 14 introduced species of the family Lumbricidae *Allolobophora caliginosa* is the one we are most concerned with in pasture improvement, and references to beneficial earthworms will be confined to this species, unless otherwise stated. *Eisenia rosea* and *A. chlorotica* also appear to be beneficial but are of lesser importance. *Lumbricus rubellus* is widely distributed and is often found in areas not populated with *A. caliginosa*, without beneficial effects being noticeable. Species that are not beneficial are, however, of importance in one sense: one or other of them occur in most places, thus misleading farmers and others into believing that introduction of beneficial species is not required.

AREAS NOT POPULATED

The distribution of beneficial species has been studied by Nielson (1951a, 1962a) who has found *A. caliginosa* to be absent from many soils because calcium levels are too low (4 milliequivalents % or less). On the other hand, some soils with adequate calcium levels have remained unpopulated simply because beneficial species have not been introduced, either intentionally or by accident. In some localities inadequate soil moisture has limited both the extent and density of populations.

Although no estimate of the area remaining unpopulated by beneficial species may be made, it includes most of the upland and high country yellow-brown earths of the South Island, and probably other strongly leached soils in which calcium levels have not been raised by liming. Extensive areas of these soils have been developed into improved pastures but, although limed to a level adequate for *A. caliginosa*, many have remained unpopulated for over 20 years. Much greater areas remain to be developed, both privately and by the State.

In the North Island, Nielson (1964) has found beneficial earthworms to be absent from large areas of pumice soils, although there is evidence that conditions are suitable for their establishment even when calcium levels are low by normal standards. He estimates, for instance, that about half of Rotorua County is so affected.

Beneficial earthworms are absent, then, from considerable areas of undeveloped, partly developed and otherwise highly developed land. In addition there are probably much greater areas where beneficial species are present, but where their effectiveness is limited by marginal calcium or moisture levels.

EFECTS ON PASTURE PRODUCTION

The beneficial effects of suitable earthworms on soil fertility and pasture production have been recognised by observers in various parts of New Zealand for many years, and have been reported by Hamblyn and Dingwall (1945), Nielson (1951a, b, 1953, 1962a), Waters (1951), Sears and Evans (1953), Richards (1955) and Stockdill (1959).

Nielson (1951b, 1953), in turf and pot trials using eight different soils, demonstrated increases in production associated with the presence of *A. caliginosa*. Measured over a 20-month period increases ranged from 28% to 110% and were attributed, in part at least, to a growth substance secreted by the worms. The lower increases were from soils that had been populated with worms for many years before being used in the trial.

Waters (1951), again in pot trials, showed that the addition of earthworms increased the yield of ryegrass alone by 77% and of the ryegrass component of a grass/clover mixture by 113%. Yields of white clover and the clover component of the mixture showed no significant increase.

Stockdill (1959) was able to measure in the field, the impact of an introduced population of *A. caliginosa* on the production of an otherwise highly developed pasture, on an hygrous upland yellow-brown earth near Hindon, Otago. The trial field had been ploughed from virgin snowgrass (*Chionochloa* spp.) and fescue tussock *(Festuca novae-zealandiae)* in 1940, put through a rotation of fodder crops, and sown to pasture with kale in the spring of 1943. It received 1 ton of burnt lime in 1941, and again at sowing in 1943. One ton of ground limestone was applied in 1945. It has been regularly topdressed with superphosphate and has had periodical applications of molybdenum and DDT.

The pasture produced well in the first few seasons and was capable of carrying 8 sheep per acre during the spring and summer. Closed for hay in December 1945, the two-year-old pasture produced a hay crop of 80 bales per acre in March, 1946. There was some grass-grub *(Costelytra zealandica)* damage in intervening years but the field was still regarded as high-producing in October 1949 when the earthworms were introduced.

Four years later, in September, 1953, green patches of earlier spring growth were observed at each point of liberation. In May, 1954, areas were trimmed to even height and enclosed in wire netting frames, five where earthworms were active and five where there were none of the introduced species. Over the six month period, from May to November, production was increased by 72% as shown in Table 1. This shows that without suitable earthworms the return obtained from development, liming, topdressing, fencing and so on was only 58%, or a little better than half, of the potential.

TABLE 1. *Yield of green pasture at Hindon, Otago, from 18 May to 20 November, 1954.*

	lb. per acre
Without earthworms	9,320
With earthworms (*A. caliginosa*)	16,090
Difference (Significant 1% level)	6,770

MODE OF ACTION

How are these substantial increases in pasture production brought about? How is the fertility of the soil, and the pasture environment, modified by the presence of a vigorous earthworm population?

In the absence of beneficial earthworms residues of dung and dead plant material accumulate in a peaty layer at the soil surface and applied lime, fertilisers and insecticides remain as a surface veneer. Beneath this the soil lacks organic material and plant nutrients and is compact, of poor structure and often dry. Penetration of moisture and development of plant roots are severely restricted.

Where earthworms are active all dung, plant residues, lime, fertilisers and insecticides are incorporated into the top-soil enriching it in organic material and available plant nutrients and ensuring the necessary contact of insecticides with pasture pests. Plant growth substances are secreted and pass into the soil. The soil structure is improved, there is better infiltration of rainfall and improved moisture-holding capacity, resulting in an obviously more friable and moister topsoil and improved root development.

Completion of Fertility Cycle:

Without earthworms fertility is locked up in the organic mat at the soil surface and there is a definite break in the "fertility cycle". Earthworms incorporate these residues of dung and dead vegetation into the soil so enabling the completion of the cycle in which, according to Sears (1953), "Plant nutrients pass rapidly and frequently from soil to plant to animal to soil and so on". The figures for loss on ignition, organic carbon and nitrogen, from Table 2, show clearly that organic matter has been removed from the surface and incorporated into the soil beneath. Cation exchange capacities of the surface and deeper layers have been modified in line with organic matter transfer.

That earthworms (mainly *A. caliginosa*) do in fact feed on dung, dead plant roots and partly decomposed herbage has been shown by Waters (1951) who also found that fresh grass and clover fed at the surface remained relatively untouched until they reached the moist brown wilt stage.

Vertical Distribution of Fertilisers and Lime:

Chemical analyses indicate better vertical distribution of fertilisers and of lime in particular on areas with worms. Figures for total exchangeable bases, base saturation and exchangeable calcium are in line with transfer from the surface to the deeper layers.

Numerous liming trials have shown that, in the absence of earthworms, lime remains concentrated at the surface. Lime applied at rates

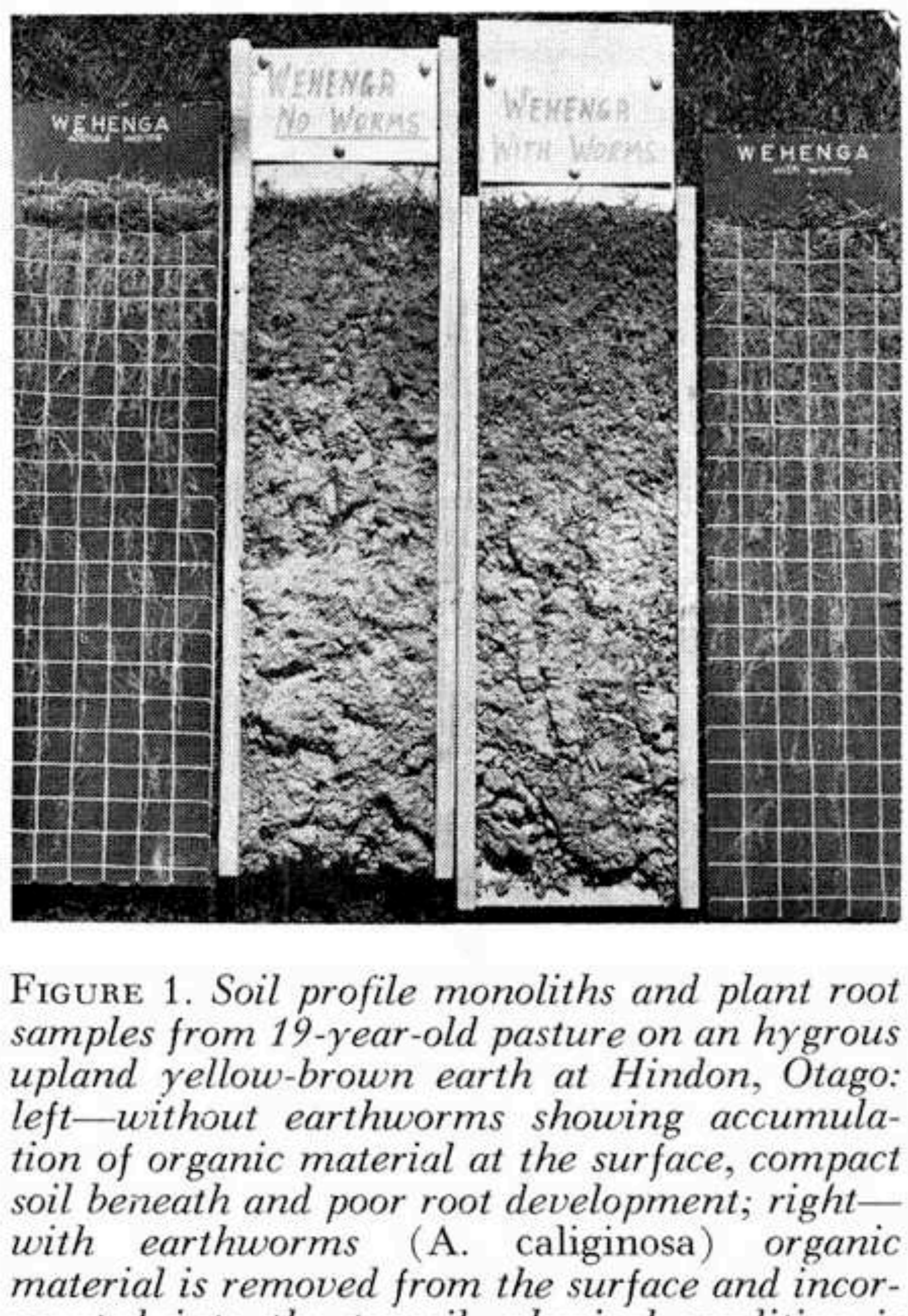

FIGURE 1. *Soil profile monoliths and plant root samples from 19-year-old pasture on an hygrous upland yellow-brown earth at Hindon, Otago: left—without earthworms showing accumulation of organic material at the surface, compact soil beneath and poor root development; right—with earthworms* (A. caliginosa) *organic material is removed from the surface and incorporated into the topsoil, physical condition is improved and topsoil is blended with subsoil.* (Prepared by E. J. B. Cutler, photo by R. W. Cooper.)

TABLE 2. *Chemical analyses of soil samples taken in May 1955 from an hygrous upland yellow-brown earth at Hindon, Otago.*

Depth in inches	Exchangeable cations in milli-equivalents %							pH	Organic matter		
	*CEC	†TEB	Ca	Mg	K	Na	% base saturation		C%	N%	Loss on Ignition %
	Without earthworms										
0–1	27.9	24.7	20.0	3.0	1.22	0.48	89	6.3	7.6	0.616	17.1
1–3	17.3	10.3	8.6	0.9	0.46	0.32	60	5.6	3.6	0.288	9.6
3–6	15.5	5.9	4.8	0.5	0.28	0.25	38	5.5	2.7	0.226	8.2
6–9	12.5	2.0	1.5	0.2	0.16	0.13	16	5.3			
	With earthworms										
0–1	23.7	19.4	15.2	2.6	0.99	0.61	82	6.0	6.0	0.498	14.6
1–3	19.5	12.0	10.4	0.9	0.33	0.30	62	5.9	4.0	0.337	10.6
3–6	16.2	8.3	7.0	0.8	0.22	0.27	51	5.8	3.1	0.254	8.8
6–9	13.5	2.3	1.8	0.05	0.19	0.21	17	5.3			

*CEC = Cation-exchange capacity. †TEB = Total exchangeable bases.

up to 40 cwt. per acre has invariably had very little effect below the top inch, even after 4 to 5 years.

Vertical Distribution of Insecticides:

Earthworms also appear to be necessary, at least on some soils, for the satisfactory vertical distribution of D.D.T. Failures in grassgrub control have been associated with absence of earthworms. Tests on an hygrous upland yellow-brown earth soil at Macrae's Flat, Otago, have shown that, 2½ years after application, 95% of the D.D.T. present has remained in the top half-inch (Table 3). Similar results are reported by Doak (1962, 1963, 1964) for two North Island volcanic soils, Mairoa Ash and Taupo Ash, on which grassgrub control had been unsatisfactory. Doak refers to "poor earthworm activity" and the formation of a "peaty topsoil overlay" and it is probable that no beneficial earthworms were present.

TABLE 3. *Vertical distribution of D.D.T. in an hygrous upland yellow-brown earth without earthworms at Macrae's Flat, Otago, 2½ years after application.*

Depth in inches	D.D.T. in p.p.m.
0–½	22.0
½–1	0.5
1–3	< 0.5

Tests by Perrott (1964) have shown grassgrubs from an area at Macraes Flat to be susceptible to D.D.T., thus eliminating an earlier suggestion that poor control was due to D.D.T. resistance. Analyses of soil from various depths again showed concentration of D.D.T. at the surface (Table 4) and, in a bio-assay in which grubs were exposed to soil from various layers, only soil from the top inch gave satisfactory control. This, in turn, indicated that poor control resulted from surface concentration of the D.D.T. and not from either its breakdown or its non-availability because of adsorption.

TABLE 4. *Vertical distribution and effectiveness of D.D.T. in an hygrous upland yellow-brown earth without earthworms at Macrae's Flat, Otago, 15 months after application.*

Depth in inches	D.D.T. in p.p.m.	% of grassgrub larvae affected on exposure to soil from various depths.
0–1	27.2	92
1–2	1.25	8
2–3	0.64	6

That earthworms do influence the downward movement of D.D.T., and its effectiveness in controlling grassgrubs, is shown in Table 5. Here, parts of a field with and without worms are compared two years after D.D.T. treatment. It is almost certain that in the absence of earthworms poor grassgrub control on these soils results from D.D.T. failing to contact the larvae.

TABLE 5. *Grassgrub control and vertical distribution of D.D.T. in a subhygrous yellow-grey earth at Nenthorn, Otago, 2 years after application.*

		Without earthworms	With earthworms (60 per sq. ft.)
Grassgrub larvae per sq. ft.		40	nil
D.D.T. in p.p.m.	0″–½″	20.0	11.0
	½″–1″	1.8	6.4
	1″–3″	0.1	0.2

Plant Growth Substances:

Nielson (1965a, b) has detected plant growth substances in eight species of the family Lumbricidae and in two introduced species of the Megascoloidae. His evidence indicates that these growth substances are the product of earthworm metabolism, that they are secreted into the alimentary tract and later voided in the faeces. Fresh casts were found to be active. As the substances have not yet been isolated in purified form it has not been possible to verify their effect on soil fertility and pasture production.

Physical Changes and Soil Moisture:

In their natural state the yellow-brown earths in particular are of good structure and absorb moisture readily. Cultivation destroys this good natural structure and, in the absence of earthworms, heavier stocking of sown pastures consolidates the top-soil to the point where moisture penetration is severely restricted. Both run-off and susceptibility to drought are increased.

Wherever beneficial earthworms *(A. caliginosa)* have invaded pastures free of worms soil structure has improved and there has been better infiltration of rainfall. The results of moisture tests on soils from various areas have borne this out but recent field investigations by Cossens (1965) are of particular interest. In all, he has six sites with and without *A. caliginosa* under investigation and results from Sites 1 and 2 are presented in Tables 6, 7 and 8.

TABLE 6. *Physical analyses and soil moisture data for site 1, an hygrous upland yellow-brown earth at Hindon, Otago, and site 2, a subhygrous yellow-grey earth at Nenthorn, Otago.*

		SITE 1. Y.B.E.			SITE 2. Y.G.E.	
Property	Depth in inches.	Pasture without worms.	Pasture with worms	Tussock without worms	Pasture without worms	Pasture with worms
Field capacity	0–4	42.0	51.7	47.4	33.2	36.6
% by weight.	0–12	36.6	42.7	40.8	28.2	33.1
15 bar retention	0–4	15.6	16.2	16.9	10.2	11.7
% by weight.	0–12	13.5	13.7	14.2	9.0	9.6
Bulk density	0–4	0.68	0.86	0.78	0.90	0.99
gms/cc.	0–12	0.96	0.96	0.94	1.09	1.13
Available moisture	0–4	0.72	1.22	0.95	0.83	0.99
in inches.	0–12	2.60	3.31	2.95	2.48	3.18
Macro porosity	0–4	44.9	21.5	30.9	45.3	25.5
%.	0–12	29.3	22.7	26.2	31.4	19.6
Organic carbon	0–4	3.54	4.46	4.62	2.60	3.68
% by volume.	0–12	2.38	2.97	2.77	2.10	2.80
Infiltration in inches.						
5 hour intake.		11.40	23.95	16.55	6.50	11.79
Basic rate per hour.		0.55	1.04	0.56	0.51	1.00

TABLE 7. *Inches of available moisture in the 0–12 inch soil depth for site 1 at Hindon, Otago, and site 2 at Nenthorn, Otago, at various dates.*

	SITE 1. Y.B.E.			SITE 2. Y.G.E.	
	Pasture without worms	Pasture with worms	Tussock without worms	Pasture without worms	Pasture with worms
June 1964	3.12	3.33	3.86	1.62	1.83
August 1964	2.60	3.30	3.35	1.29	1.41
November 1964	0.98	1.33	1.59	0.61	1.02
February 1965	2.19	2.53	2.47	0.96	1.83

TABLE 8. *Effect of earthworms on leaching as revealed in quick test analyses of soil from site 1 at Hindon, Otago, and site 2 at Nenthorn, Otago.*

	SITE 1. Y.B.E.				SITE 2. Y.G.E.			
Depth in inches	Without worms		With worms		Without worms		With worms	
	pH	Ca	pH	Ca	pH	Ca	pH	Ca
0–4	5.9	10	5.5	6	6.9	14	5.8	9
4–8	5.8	7	5.4	5	6.1	10	5.2	3
8–12	5.3	1	5.1	1	4.9	2	5.0	1

Site 1: Samples taken 19 years after liming and 10 years after invasion of effective earthworm population.
Site 2: Limed within 4 years of sampling.

Site 1 is the Hindon field used for the earlier pasture production measurements and is an hygrous upland yellow-brown earth soil. Counts show 96 *A. caliginosa* and 10 *L. rubellus* per square foot for the area with worms, and only an odd native for that without. The "tussock" area, included for comparison, is an unploughed snowgrass/fescue tussock association, bordering the sown pasture. It has not been limed, but will have been modified to some extent by the increased level of stocking and some transference of fertility.

Site 2 is a thirteen-year-old pasture on a subhygrous yellow-grey earth soil at Nenthorn, Otago. It received 1 ton of lime at sowing in 1952, ½ ton in 1956, and again in 1961. The area supporting worms has shown 58 *A. caliginosa* and 6 *Octolasium cyaneum* per square foot with an odd native and *L. rubellus*. That without introduced worms has a population of 19 per square foot of a slender native species that is having no apparent beneficial effect.

The *field capacity* (determined in the field) of the soils with worms is higher at both sites. For the 0–12 in. depth at Site 1 the increase is 5% over the "tussock" and 17% over the pasture without worms. At Site 2 the increase is also 17% over worm-free pasture. This higher field capacity is probably the result of increased organic matter combined with vastly improved structure in the soils with worms, as compared with those without. The "tussock" also has a good natural structure and high organic content. The figures for organic carbon confirm the higher levels of organic matter in the soils with worms and the "tussock".

The *15 bar retention* (determined in the laboratory from disturbed cores) is taken as a measure of wilting point. Areas with worms are only slightly higher than those without and the "tussock" slightly higher than pasture with worms.

Changes in *bulk density* may be largely attributed to the presence or absence of turf mat. Depending on the period of residence of *A. caliginosa* this mat may be partially or completely removed, and incorporated into the topsoil. The bulk density of all soils is about the same for the 0–12 in. depth, the most significant changes occurring in the 0–4 in. region with the wormy soils somewhat higher.

The *available moisture* capacity is calculated from the field capacity, the 15 bar retention and the bulk density. The soils with worms show a marked improvement, having the capacity to hold approximately 0.7 inches more available moisture in the 0–12 in. depth when compared with soils without worms. The "tussock" is intermediate.

Infiltration rates were determined with double ring infiltrometers, both "dry" and "wet" runs being made. The 5-hour intake is the amount of water taken in during the first 5 hours of the initial or "dry" run. The basic rate is taken as the intake for the third hour of the second or "wet" run. In each instance means of results from six infiltrometers show almost double the rate of infiltration in the presence of earthworms. Results from four additional sites show a similar trend although the differences, particularly for the basic rate, are smaller.

The greatly increased rates of water intake of the soils with worms, and to a lesser extent the increased final infiltration, or basic rate, is a reflection of the marked improvement in soil structure.

The *macro-porosity* of the soils with worms has decreased markedly, and this is, at first sight, difficult to reconcile with the increased infiltration rate. However, structure has improved in the presence of earthworms and it is likely that there are fewer macropores of greater diameter, thus allowing freer movement of water.

The *actual available moisture* throughout the year is influenced by both infiltration rate and available moisture capacity of the soil. Periodic testing has shown (Table 7) that the soils with worms maintain a much better moisture status than those without at all times.

Results for the "tussock" are at times higher than for the pasture with worms, but moisture status of the "tussock" could be influenced to some extent by microclimatic factors such as condensation of dew or by the uneven nature of the soil surface.

It follows that where tussock areas are developed into sown pastures, without suitable earthworms, there will be a significant increase in the rate of run-off and the consequent risk of soil erosion and flooding. A moisture conservation and run-off control programme based on the encouragement of earthworms could be preferable, or complementary, to contouring. With earthworms, the local concentration of moisture that occurs with contouring would be avoided or minimised.

Root Development:

Improved soil structure, better moisture penetration, deeper incorporation of plant nutrients and organic material and better control of grassgrub all contribute to greatly improved root development. This further reduces susceptibility to drought, enables better utilisation of nutrients and makes production over high and low rainfall periods more uniform.

Increased Leaching:

The earlier chemical analyses showed the beneficial effect of better incorporation of lime into the top-soil in the presence of earthworms. However, the more recent quick test analyses obtained by Cossens show (Table 8) much lower pH and calcium levels for the wormy soils down to 12 inches.

This more rapid loss of lime has no doubt been brought about by the increased leaching that must be associated with the higher infiltration rates. It follows that wormy soils will require higher levels of maintenance liming than soils without worms.

TABLE 9. *Quick test analyses, earthworm numbers and moisture content of low and high lime strips on a Warepa soil at Flag Swamp, Otago.*

Depth in inches	Quick tests pH	Ca	Worms per sq. ft. *E. rosea*	*A. calig.*	*L. rub.*	Moisture %
Low lime, pasture poor and soil dry.						
0–3	5.5	5	30	2	-	19.2
3–6	5.6	4				12.2
High lime, pasture good and soil moist.						
0–3	6.5	10	86	4	2	33.3
3–6	6.1	6				24.8

(All figures are means of samples from 4 sites on each treatment taken on 12/5/62, 6 years after application of lime.)

THE IMPORTANCE OF LIME

Nielson (1951a, 1962a) has found that *A. caliginosa* requires at least 5 m.e.% of calcium and that populations increase with higher calcium levels. In a pot trial lasting 10 months he (1962b) has shown numbers of *A. caliginosa* to increase, from reproduction alone, by 50% in response to 1 ton of lime and by 90% in response to 2 tons. This evidence is supported by five field trials in the Palmerston area of Otago where earthworms increased by 50% in response to 1 ton of lime per acre. Pasture responses were associated with improved soil moisture.

On a Warepa soil near Flag Swamp, Otago, uneven application of lime emphasized the differences in soil moisture content and pasture growth that can result from earthworm stimulation by heavier liming. Earthworm numbers, mainly *E. rosea*, increased threefold and the difference in soil moisture was remarkable (Table 9). Here the moisture differences have been exaggerated, run-off from the poor areas being absorbed in the good strips. There could also have been some migration of earthworms. However, the effects again point to the importance of earthworm activity, stimulated if necessary by liming, in the conservation of moisture and the control of run-off.

CONCLUSION

The beneficial effects of certain introduced earthworms, mainly *A. caliginosa*, have been demonstrated. Pasture production increases of more than 70% have resulted from earthworm activity but considerable areas of New Zealand remain unpopulated by beneficial species.

Physical, chemical and biological changes are involved in the improvement of the pasture environment: Plant residues and animal excreta are incorporated into the soil thus enabling the completion of the "fertility cycle". Lime and fertiliser are similarly incorporated. Better vertical distribution of D.D.T. insecticide gives improved control of grassgrub. Plant growth substances are secreted, although their effect on produtcion has not yet been measured. There is a marked improvement in soil structure, infiltration rate, moisture-holding capacity and plant root development.

In soils supporting populations of introduced earthworms more rapid leaching and high calcium requirement of earthworms indicate the need for a higher level of maintenance liming than is necessary on soils without worms.

A vigorous earthworm population is of importance, not only in the attainment of higher levels of pasture production, but also in the conservation of moisture, the control of run-off and the avoidance of soil erosion and flooding.

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EFFECTS OF GRASS GRUB INFESTATIONS ON PASTURE

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INTRODUCTION

In considering the effects produced on pasture areas by infestations of grass grub, it is important to bear in mind certain aspects of its biology:

The insect commonly known as grass grub is the melolonthine beetle *(Costelytra zealandica)*. Other species of the same sub-family are sometimes also found in pasture, especially species of *Pyronota* (manuka beetle). The economic importance of these is however minor and this paper is concerned solely with *C. zealandica.*

The grass grub is univoltine, though there is some evidence that a certain percentage of populations at least may spend two years in the larval stage in the southernmost parts of the South Island. Adult beetles emerge in spring and live for two or three weeks. Eggs are laid in the soil and take two to three weeks to hatch. The resultant larvae pass through three instars and are actively feeding for most of the time from hatching to pupation, i.e. for about eight or nine months of the year.

In the absence of control measures, grass grub infestations tend to persist in the same place year after year, probably due to the early flight pattern of males and resultant mating of females and oviposition in the area from which they emerged.

Adult beetles will feed readily on the foliage of a wide range of plants but it is unlikely that they need to feed before they are sexually mature. Stone-fruit trees in particular may sometimes be almost stripped of foliage but any feeding by adult beetles on species of pasture plants is unimportant.

There is a wide range of feeding habits among scarabaeid larvae but *C. zealandica* feeds exclusively below ground on the roots of plants. Considerable amounts of soil are ingested and pass through the body with the plant root material.

The third instar occupies most of the larval life span and is present in the soil from about March through to September in most districts and it is usually during this period that visible damage to pastures occurs.

EFFECTS OF INFESTATION ON PASTURE

There are at least two and possibly three distinct facets to the depredations caused by grass grub larvae in pastures. These are:

(a) direct loss caused by larval feeding on roots of pasture species.
(b) changes in pasture composition, principally weed invasion, resulting from selective feeding and/or ability of weeds to withstand attack, and
(c) possible effects on soil.