OBSERVATIONS ON TWO ANIMAL EXCLOSURES IN HAURANGI FOREST OVER A PERIOD OF TWENTY YEARS
(1951-1971)

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SYNOPSIS

In two exclosures established in Haurangi Forest to exclude ungulates, opossums have not affected recovery of the vegetation. Although within the exclosures recovery was initially slow, after ten years a complete canopy had formed, with litter and humus accumulation, and after 20 years a canopy replacement layer had formed which has ensured the perpetuation of the forest type. Outside the exclosures, in spite of large reductions in animal numbers, little response was seen other than the slow growth of unpalatable tree ferns.

INTRODUCTION

Early results from field investigations on opossums indicated that the interaction of opossums with deer and other ungulates was detrimental to the protective values of many indigenous forests (Kean and Pracy, 1948; Pracy and Kean, 1949). However, in the absence of ungulates, it was considered that opossums did not cause significant damage, except to certain forest types, and that they did not impair natural regeneration or restrict replacement of tree or shrub species. So it was decided to erect exclosures, in badly depleted forest types, two of which were established (in 1951 and 1959) in the Pararaki catchment, Haurangi Forest (Fig. 1). They were to be used to determine whether regeneration and survival of seedlings would occur in the presence of high opossum numbers and also to determine the effectiveness of current animal control operations by a comparison of the vegetation inside the exclosures with that outside.

THE STUDY AREA

The Haurangi Forest is about 65 km east of Wellington, near Cape Palliser. The parent rock is predominantly greywacke and the soils are thin, stony and prone to erosion. The vegetation is a mosaic of podocarp forest in the wetter areas and

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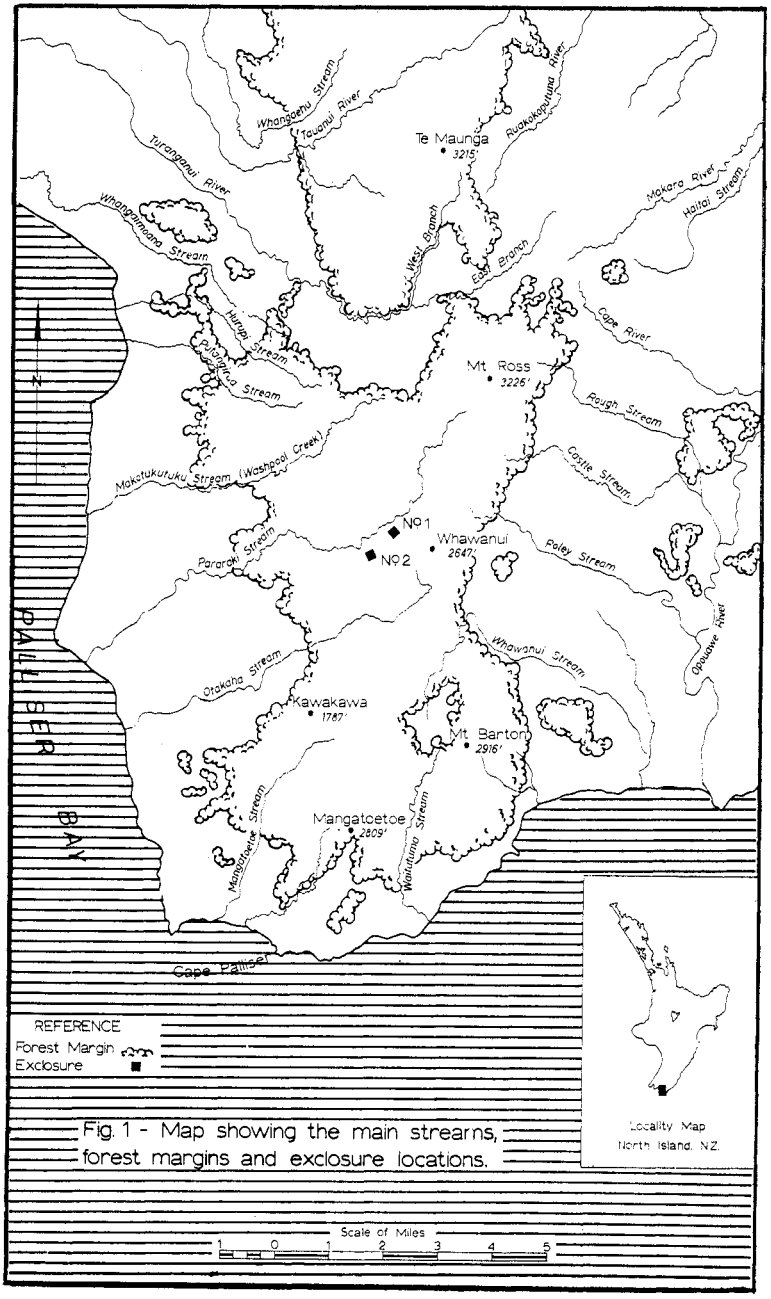

Fig. 1 - Map showing the main streams, forest margins and exclosure locations.

FIG. 1: *Map showing the main streams, forest margins and exclosure locations.*

black beech *(Nothofagus solandri)*, red beech *(N. fusca)* and silver beech *(N. menziesii)* forest (Wardle, 1967).

Depletion of the ground and shrub tier vegetation was progressive from late in the 19th century as goats, then subsequently pigs, deer and, to a lesser extent, cattle and sheep, became established. The deterioration of the forest had reached an advanced stage (Fig. 2) before opossums became established. Dispersion and complete colonization of the forest by opossums (1920-1940) was followed by the depletion of many preferred canopy and sub-canopy species in 1940-50. In 1951, when the first exclosure was erected (Fig. 2) the forest consisted of a few widely spaced old individuals, few co-dominants, and replacement seedlings which were consistently browsed and killed by ungulates. These conditions remained unaltered in spite of control operations conducted by the Wildlife Branch of the Internal Affairs Department from 1949 onwards. In 1960-65 intensive operations reduced goat numbers to low levels, completely eliminated wild sheep, but were less effective in reducing the populations of deer and pigs. As a result, vegetation response is now apparent, especially on the steep faces formerly favoured by goats.

FIG. 2: *Typical view of forest floor when first exclosure was erected in 1951.*

THE EXCLOSURES

Exclosure No. 1 is on a small flat on a steeply ascending ridge about 150 m above the Pararaki Stream, at an altitude of about 330 m. The site is in the transition zone (ecotone) between podocarp and black beech forest. Since the exclosure was erected in 1951 the canopy has been opened by the death of rewarewa *(Knightia excelsa)* and other trees of the podocarp forest element, leaving a canopy consisting of a

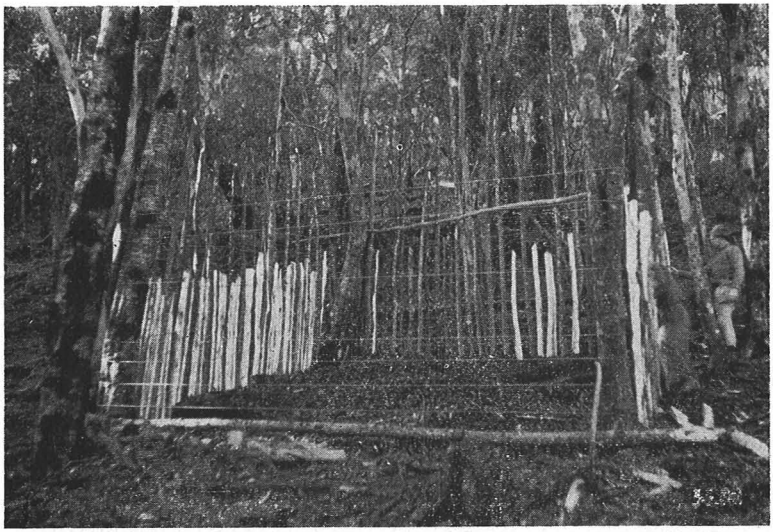

FIG. 3: *Exclosure No. 1 under construction in 1951*
(Photo by J. Ollerenshaw)

few widely spaced black beech trees. The area is a rough rectangle (40 m^2) and the fence is 2.1 m high, with lower wires spaced at 20 cm intervals. The closely-spaced battens (Fig. 3) decayed rapidly and were overlain with 76 mm mesh netting in 1958. The close mesh was to ensure that young goats and pigs could not get in.

FIG. 4: *Exclosure No. 2 at time of erection in 1959.*
(Photo by J. H. Johns)

Exclosure No. 2, erected in 1959, is on a small stream terrace about 10 m above a tributary of the Pararaki Stream, at a similar altitude to No. 1 exclosure. The site is again in the podocarp/beech ecotone, but under a hinau *(Elaeocarpus dentatus)* canopy. This exclosure is almost rhomboid, enclosing 100 m^2, and here the fence is more open than at the original exclosure, with wires spaced at 40 cm intervals to 2 m height supporting 76 mm mesh wire netting (Fig. 4).

VEGETATION RESPONSE

Lists of species and the heights of the tallest plants were recorded annually to follow the progressive colonization within the fenced areas. In 1959 detailed recordings of heights and densities were made within the exclosures and similar-sized adjacent control areas. Similar detailed measurements were made in 1960, 1961 and 1971.

When exclosure No. 1 was erected only one seedling of raurekau *(Coprosma australis)* was present inside it and the ground outside was bare. In the first year after the fence was erected over 80 seedlings of raurekau appeared, and a few seedlings of seven other species. None of these was over 8 cm tall and many were short-lived. In the subsequent years the number of species continued to increase, although some species survived for only a year or two. By 1959, of the 30 species that had occurred, only 21 were established. Although raurekau rapidly became dominant because of its large size and rapid growth rate, it made up less than 20% of the plant density in 1959 (Table 1), as there was a large population of ephemeral seedlings of other species, mainly rewarewa and hinau. At the same time, only 30% of the seedlings were over 15 cm tall. Most of these were raurekau.

Seedlings had also survived outside the exclosure, mainly in the shelter of roots and ground irregularities, as a result of animal control operations. In 1959, seedling density outside the exclosure was about half that within, but only 11% of the seedlings were over 15 cm tall and few were persistent. The large turnover in seedlings outside the exclosure was apparently caused by continued browsing pressure.

The next two years were evidently good seed years, as the plant density within the exclosure doubled — there were also large changes at No. 2 exclosure at this time — but most of the seedlings did not persist. During the second ten years (1961-71) the number of species rapidly declined to 17 as ephemeral species were suppressed. Numbers then increased as fern species appeared. At the same time, the density of raurekau increased slightly, but that of all other species declined, contributing to a fall of 60% in total density. Fifty-five percent of the mortality occurred in the < 15 cm height class and there were striking declines in the frequencies of *Coprosma lucida* (eliminated), lemonwood *(Pittosporum eugenioides)* and putaputaweta *(Carpodetus serratus)*. Mahoe *(Melicytus ramiflorus)*, matipo *(Myrsine australis)* and hinau increased in the > 15 cm height class. Competition and insect damage appeared to be strong forces in the reduction of

TABLE 1: SEEDLING DENSITIES, BY SPECIES, INSIDE AND OUTSIDE EXCLOSURE No. 1 AT THE FOUR MAJOR REMEASUREMENTS

	Density ('000/ha)							
	Inside Exclosure				Outside Exclosure			
Species	1959	1960	1961	1971	1959	1960	1961	1971
Elaeocarpus dentatus	3.85	18.19	19.35	0.91	3.15	3.73	1.95	4.39
Coprosma australis	4.76	5.26	5.27	4.01	1.11	0.91	0.75	1.82
Nothofagus solandri		0.08	0.04	0.04	0.25		1.41	8.74
Pittosporum eugenioides	3.27	3.81	3.39	0.37	0.12	0.50	0.25	0.21
Myrsine australis	0.91	2.03	1.66	1.16	0.25	0.16	0.08	1.16
Hedycarya arborea	0.50	1.70	1.33		0.41	0.87	2.90	0.12
Eugenia maire	1.16	3.31	2.28	0.33	0.08	0.21	0.21	0.21
Rhipogonum scandens	0.91	1.37	1.49	0.50		0.08	0.12	
Knightia excelsa	0.91	2.15	1.57	0.04	0.25	0.12	0.37	
Coprosma rhamnoides	1.57	1.86	1.78	0.04	0.46	0.91	0.21	1.12
C. robusta	1.49	0.70	0.54					0.79
Macropiper excelsum	0.50	0.54	0.37		0.41	0.12	1.20	
Melicytus ramiflorus	0.79	0.46	0.33	0.54	0.54	0.54	0.33	0.21
Uncinia uncinata	0.33	0.21	0.29	0.17	0.12	1.12	1.12	3.96
Persoonia toru	0.16	0.37	0.37	0.13				0.12
Carpodetus serratus	0.49	0.58	0.53	0.08	0.29	0.58	0.75	0.12
Podocarpus ferrugineus		0.33				0.12	0.04	
Hebe salicifolia					0.04		0.08	0.04
Cyathodes fascicularis					0.04		0.17	0.04
Cassinia retorta								0.04
Aristotelia serrata	0.16	0.41	0.04		0.04	0.17		0.04
Cyathea dealbata	0.04			0.04	0.08			
Polystichum richardii				0.08				
Senecio jacobaea								0.54
Carsium spp.				0.08				0.04
Galium sp.								0.04
Microlaena avenacea								0.04
Hydrocotyle sp.								0.04
Mean density	22.29	45.92	41.32	8.45	10.32	15.30	10.32	24.30

plant densities, while micro-environmental changes seemed to favour the increases in the second group of species, which now form a prominent second tier at 30 to 60 cm height. Rate of height growth of the taller raurekau has declined since 1960. This appears partly because at 5 m the plants are approaching their maximum height and partly because the plants appear to be intolerant of the increased exposure and light reaching the shrub layer through canopy gaps caused by the death and subsequent windthrow of several trees near the exclosure in 1968. This latter effect is borne out by the chlorotic appearance of the leaves.

In the same period (1961-71) the changes outside the exclosure have been marked, especially since the windthrow of 1968. There are now as many seedlings over 15 cm tall as there were (and are) below this height although few are yet over 45 cm tall. The most abundant species, hinau, matipo

TABLE 2: SEEDLING DENSITIES, BY SPECIES, INSIDE AND OUTSIDE EXCLOSURE No. 2 AT THREE MAJOR REMEASUREMENTS

	Density ('000/ha)					
	Inside Exclosure			Outside Exclosure		
Species	1959	1961	1971	1959	1961	1971
Elaeocarpus dentatus	2.48	10.82	1.09	4.48	3.58	0.66
Hedycarya arborea	0.76	3.19	1.47	0.18	2.25	0.07
Knightia excelsa	10.57	3.15	0.30	0.38	0.28	0.30
Rhipogonum scandens	0.38	2.18	1.07	0.23	1.37	0.13
Eugenia maire	1.09	2.63	2.31	0.59	0.64	0.69
Urtica ferox	0.26	1.42	0.13	0.12	0.38	0.03
Uncinia uncinata	0.45	2.25	0.43	0.53	1.54	1.25
Macropiper excelsum	0.20	1.02		0.18	0.89	0.03
Coprosma australis	0.38	0.56	0.78	0.77	0.85	0.08
Myrsine australis	0.16	0.51	1.11	0.03	0.18	0.07
Carpodetus serratus	0.17	1.06	4.62	0.21	0.56	0.62
Parsonsia heterophylla	0.83	0.16	0.03	0.03	0.05	0.03
Pittosporum eugenioides	0.15	0.28	0.66	0.21		0.50
Melicytus ramiflorus	0.13	0.23	0.43	0.03	0.23	0.28
Coprosma rhamnoides	0.13	0.21		0.03	0.03	0.03
C. robusta	0.01					
Metrosideros robusta			0.13			
Podocarpus ferrugineus	0.12	0.16	0.16	0.02	0.05	0.23
P. spicatus			0.07			
Schefflera digitata						0.03
Pennantia corymbosa					0.02	0.07
Pseudopanax crassifolium						0.02
Pseudowintera colorata			0.10		0.03	0.02
Aristotelia serrata					0.03	
Cardamine debilis			0.10			
Microlaena avenacea			0.10		0.03	
Cordyline banksii					0.03	
Geranium spp.	0.24					
Ranunculus hirtus	0.03	0.03		0.15	0.17	
Clematis spp.		0.08	0.13		0.05	
Cyathea smithii			0.02	0.15	0.10	0.02
C. dealbata	0.05	0.15	0.02	0.08		0.17
Polystichum richardii	0.05	0.18	0.05		0.08	0.03
Asplenium flaccidum	0.03	0.28	0.08			0.01
A. bulbiferum			0.13			
A. lucidum		0.03	0.02			
Ctenitis velutina			0.80			0.50
Blechnum filiforme	0.07	0.07	0.07			
B. lanceolatum						0.02
Hypolepis millefolium		0.02	0.20	0.02	0.13	0.20
Pellaea rotundifolia	0.08	0.02				0.02
Lindsaea viridis	0.03	0.74	0.23		0.15	0.10
Pyrrosia serpens			0.03			
Histiopteris incisa			0.10			
Mean density	18.65	31.61	12.19	8.51	13.78	5.44

and black beech, are not highly palatable and many of the other species — *e.g., Cyathodes fascicularis, Coprosma rhamnoides* — are of low palatability. Thistles *(Cirsium* spp.) and ragwort *(Senecio jacobaea)* are also common, further indicating a large increase in the light reaching the forest floor. The stage of development now is similar to that within the exclosure after three or four years (1954-55). However, the highly palatable species such as raurekau (that were the dominants) are still heavily browsed and attain maximum height only in the shelter of patches of less palatable plants such as beech, or alongside large roots and at the bases of trees.

Exclosure No. 2 was established eight years after the first exclosure (1959) and by this time there was some recovery in the vegetation. A similar density of seedlings was present on the control areas outside both of the exclosures at this time (Table 2), but the density within No. 2 exclosure was much higher. This was probably due to the proximity of a large hinau and the greater abundance of rata *(Metrosideros perforata)* offering shelter to the seedlings. There were no

TABLE 3: AVERAGE HEIGHTS OF PLANTS INSIDE AND OUTSIDE THE TWO EXCLOSURES IN 1971 AND DENSITIES FOR THE TWO HEIGHT GROUPS AT No. 1 EXCLOSURE

	No. 2 Exclosure		*No. 1 Exclosure*			
	Heights (m)		*Heights (m)*		*Densities Outside ('000/ha)*	
Species	*Inside*	*Outside*	*Inside*	*Outside*	*> 15 cm*	*< 15 cm*
Elaeocarpus dentatus	0.45	0.15	0.45	0.25	2.79	1.61
Coprosma australis	3.04	0.15	3.04	0.30	0.68	1.13
C. rhamnoides			0.15	0.45	0.12	1.01
C. robusta				0.30	0.08	0.04
Eugenia maire	1.35	0.45	0.75	0.30	0.08	0.12
Pittosporum eugenioides	2.65	0.15	0.90	0.15		0.20
Melicytus ramiflorus	1.90	0.15	0.60	0.25	0.04	0.16
Rhipogonum scandens	Adult	0.15	0.60			
Myrsine australis	0.91	0.15	0.91		1.29	0.64
Knightia excelsa	0.50	0.15	0.79	0.15		
Persoonia toru			0.45		0.04	0.08
Carpodetus serratus	2.41	1.83	0.45	0.15		0.12
Podocarpus ferrugineus	0.60	0.15				
Urtica ferox	1.00	0.25				
Nothofagus solandri			0.90	1.00	3.68	5.05
Hedycarya arborea	1.15	0.15	0.76	0.22	0.04	0.08
Uncinia uncinata	0.45	0.60	0.38	0.60	4.00	
Polystichum richardii	0.23					
Cyathea dealbata	1.80	2.13	2.13	2.28		
Asplenium bulbiferum	0.38	0.15				
A. flaccidum	0.60	0.15				
Microsorium diversifolium	0.45	0.15				

Note: Heights of ferns and grasses refer to the length of laminae or fronds.

FIG. 5: *Exclosure No. 2 in 1969, photographed from same position as Fig. 4. Note mass of* Cyathea dealbata *outside fence and* Coprosma australis *inside.*

(Photo by J. H. Johns)

seedlings over 15 cm tall and many were apparently ephemeral. This is borne out by the large changes in density of hinau and rewarewa observed over the three years 1959, 1960 and 1961.

In the 12 years at exclosure No. 2 (1959-71) raurekau rapidly became dominant (as at exclosure No. 1), but maire *(Eugenia maire)* and lemonwood were important co-dominants and matipo was a frequent sub-dominant. The growth of dominants was almost twice as fast as at No. 1 exclosure (Table 3) and that of the subcanopy species almost four times as fast. As a result there are few seedlings below 15 cm height and plant density has been halved. *Uncinia uncinata,* which was common in the early years, has been suppressed, but there is instead an increase of damp-loving ferns such as *Asplenium bulbiferum* and *Lindsaea viridis.*

Outside the exclosure, plant density has changed little since 1959 and there are no clear trends. Seedlings are still browsed back to a height of about 15 cm and the only species increasing in stature are the unpalatable tree ferns (Fig. 5).

DEVELOPMENT OF HUMUS

At the time of establishment, the forest floor at exclosure No. 1 consisted of bare stony soil. Any plant litter was blown to sheltered localities and ultimately into stream channels by storm winds. Regenerating plants inside the exclosure have tended to trap the litter. Leaf litter of appreciable depth was first recorded at exclosure No. 1 in 1957, and the build-up increased with the growth of regenerating species. Consolida-

tion and breakdown of the lower layer of litter to humus was first observed in 1963. Since 1963 the humus layer has increased in depth to 5 to 10 cm. Outside the exclosure there was little change up to 1963, but since then development of tree ferns and regeneration of seedlings has led to the formation of a very thin litter layer.

At No. 2 exclosure, in accordance with more rapid growth rates, development of humus was more rapid. By 1968 the accumulation of litter was well advanced, and by 1971 2 to 5 cm of humus had developed. Outside the exclosure, the often dense growth of tree ferns has led to some retention of a tenuous litter layer, but there is little humus accumulation.

ANIMAL DAMAGE

Although opossum faeces were recorded inside the exclosure, no defoliation by opossums was noted. Near the fence, overhanging shoots of plants were often browsed by deer or goats. The high seedling densities, however, attracted considerable insect damage, particularly by leaf miners and defoliators. This was the main cause of the decline in density of lemonwood, karamu and mahoe at No. 1 exclosure. At No. 2 exclosure, some minor damage to leading shoots of raurekau, caused by cicadas, was all that was noted.

DISCUSSION

The recovery patterns of these two exclosures are by no means exceptional. The changes at many exclosures, erected more recently on a wide variety of sites, follow a similar pattern. At No. 1 exclosure there was a brief lag before an appreciable regeneration tier formed, but in other areas the lag is more marked. Through the wide range of forest types sampled, only a few woody species attain an early dominance. These are usually the coprosmas *(C. australis, C. robusta, C. lucida* and *C. depressa),* the araliads *(Neopanax arboreum, N. simplex, Schefflera digitata), Macropiper excelsum* and *Geniostoma ligustrifolium.* These species seem to assert themselves by rapid growth and/or large leaf size, in the first two or three years. All are highly palatable to ungulates.

Rapid growth of the same groups of species was also observed after the elimination of goats on the offshore islands of Cuvier (Blackburn, 1967; Beaver *et al.,* 1969) and on Great Islands in the Three Kings (Baylis, 1951; Holdsworth, 1951; Holdsworth and Baylis, 1967). On the mainland the same patterns were seen after goat "extermination" in the Auckland Conservancy and in the Waioeka catchment (Vipond *et al.,* 1962).

Although goats have almost been exterminated from Haurangi Forest, and deer have been maintained at low numbers for over seven years, there are still sufficient animals to prevent vegetation response in most areas, as illustrated by exclosure No. 2 control area. Only if canopy opening occurs, as at No. 1 exclosure control area, will regeneration occur, and then it is restricted to species of low palatability. A simi-

lar trend of the replacement of normal canopy species by regeneration of unpalatable species, especially *Cyathea dealbata* and *C. smithii,* was also noted by the writers in the Urewera Range, at Hokitika, and many other areas. These species may form an unsatisfactory understorey, for in the event of severe defoliation of the canopy species by opossums they may not provide adequate cover for the site (Wallis and James, 1969; NZFS, 1970) so that an unstable situation as in the southern Ruahine Range (James and Beaumont, 1971) can occur, or in less severe cases it can lead to the replacement of forest by grassland (Howard, 1966).

Thus the Haurangi exclosures show that recovery in a severely depleted situation is possible with the elimination of the animals, and that the time scale of such recovery is not short. However, outside the exclosure the reduction in the animal population has not led to similar recovery, although unpalatable plants have occurred. Even with the total elimination of animals, development of the litter/soil cycle appears to take 5 to 10 years, and a new equilibrium in the understorey vegetation has not occurred in 20 years of observation at exclosure No. 1. It is evident that large changes may continue to occur for at least another 20 years. The changes outside the exclosures over 20 years can be roughly equated to those over 4 or 5 years within the exclosures, so that at the same rate of change recovery could take over 100 years.

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