ECOLOGICAL INTERACTION BETWEEN INTRODUCED AND INDIGENOUS PLANT SPECIES IN THE MANAWATU DISTRICT

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INTRODUCTION

As a result of the invasion of New Zealand by people of European origin, and by the plants and animals that they introduced, much of the plant covering of the country now consists of mixtures of native and exotic species. Smith (1957) has stated that the study of this mixed vegetation, while most of the steps in the amalgamation processes are still discernible and interpretable, is one of the most fascinating and most urgent tasks of New Zealand botanists. However, only a few workers appear to have given special attention to the subject, although the contributions of those few, notably Levy (1923), Guthrie-Smith (1926), Cockayne *et al.* (1932), and Allan (1936), are of the greatest importance. In the hope of supplementing the existing contributions, the writer has made an ecological survey of the vegetation of the Manawatu district, with emphasis on the interaction of introduced and indigenous species. The results are embodied in an unpublished thesis (Carnahan 1957), on which the present paper is based.

THE STUDY AREA

The study area covered about 600 square miles on the portion of the catchment of the Manawatu River that lies to the west of the crest of the Tararua-Ruahine Range. To permit more intensive study of the main area, certain specialised habitats were excluded. These were the coastal sands and swamps, and the region above timberline (4000 ft.). The south-west part of the area lies below about 200 ft., and is more or less flat. The land rises to the north and east from this plain, and in general becomes steeper and more broken with increasing altitude.

Mean monthly air temperatures at the Grasslands climatological station (100 ft.) range from 46° F. in July to 62° F. in January. Rainfall is spread fairly evenly through the year, and tends to increase with altitude, and with nearness to the Tararua-Ruahine Range. Mean annual rainfalls at the official rainfall stations range from 35 in. to over 100 in., and mean numbers of days with rain from 120 to over 200.

The alluvial deposits of the plains provide the parent material for a variety of recent soils. The Pleistocene and Upper Pliocene sediments of the downs and the lower hills have given rise to zonal yellow-grey earths and yellow-brown earths, or to skeletal yellow-brown earths on the steeper hillsides. Skeletal yellow-brown earths are also associated with the greywacke of the higher hills up to about 3500 ft. Above this altitude, mountain soils are found (New Zealand Soil Bureau 1948).

The early European explorers and settlers found most of the district to be covered with dense mixed evergreen forest (Buick 1903). The composition of the former forest cover may be deduced from forest reserves and forest remnants, such as those described by Allan (1924), Zotov *et al.* (1938), and Greenwood (1949). The principal podocarp was *Dacrydium cupressinum*, and the principal dicotyledonous trees were *Beilschmiedia tawa*, *Weinmannia racemosa*, and *Metrosideros robusta*. There was a great variety of other trees, and tree-ferns were also important. In the northern part of the study area, below about 1500 ft., *Nothofagus solandri*

* This work was done when the author was at Massey Agricultural College, University of New Zealand.

forest occurred on the crests of ridges and spurs, and also on gravelly faces, while *N. fusca* was present above about 1500 ft. at the northern and southern extremities.

Organised European settlement of the district began in 1871 (Buick 1903). Within about 30 years, most of the land below about 2000 ft. had been cleared of the original forest cover, and sown with English grasses and clovers.

SURVEY OF THE VEGETATION

The present vegetation was classified in terms of pastoral farming, which is the predominant kind of land-use. There are two recognisable cultural boundaries, namely the limit of cultivation and the limit of grazing, corresponding very roughly with the 500 ft. and 2000 ft. contours respectively. The vegetation within the limit of cultivation was characterised as "ploughable pasture"; that between the limit of cultivation and the limit of grazing as "unploughable pasture"; and that beyond the limit of grazing as "non-pasture".

Since it is possible to attain a relatively high degree of control over the vegetation on land that can be cultivated, it is to be expected that introduced economic species should predominate in ploughable pasture. Further, it is evident from the work of Cockayne *et al.* (1932) that in general the indigenous species may be expected to predominate on unoccupied land. Interaction between introduced and indigenous species may therefore be expected to be most intense in unploughable pasture. The form of the survey was influenced by these generalisations. The examination of ploughable pasture and non-pasture was largely confined to careful qualitative observations, whereas detailed quantitative studies were made in the case of unploughable pasture.

These quantitative studies involved estimating the frequency and cover of each plant species present in unploughable pasture, in relation to soil type, altitude, slope, orientation, and the intensity of grazing by sheep and by cattle. For sampling purposes, unit areas of relatively uniform environment were delimited, using an adaptation of the method of Greenall and Hamilton (1954). Relative grazing intensity was estimated by means of dung counts, set stocking being assumed. The estimates of frequency and cover of plant species were obtained mainly by the use of line transects, but these were reinforced by data from quadrat and point analyses. Frequency was estimated as the percentage of transects or quadrats in which the species was represented, and cover as the percentage of each transect line, or of each set of points, that was covered by the foliage of the species. The assessment of the results was complicated to some extent by partial correlations between some of the environmental factors. The effects of these factors have been separated as far as possible. (Full details of the sampling methods and of the treatment of the sampling data are given in the original thesis.)

RESULTS OF THE SURVEY

(See Appendix I)

PLOUGHABLE PASTURE

The ploughable pasture vegetation is typical high-producing sown pasture, with *Lolium perenne* and *Trifolium repens* predominating. Indigenous species are virtually absent, with the notable exception of several species of *Juncus*, which are a fairly prominent feature of the ploughable pasture of the study area. *J. polyanthemos* appears to be the principal species, and *J. luxurians* and *J. vaginatus* are also common. They are essentially weeds of long-rotation pasture, being much less common where there is an alternation of short-rotation pasture and cash crop.

UNPLOUGHABLE PASTURE

Sward-forming species

The dominant species of the sward are all perennials, comprising three introduced grasses, an introduced herb, and an indigenous grass. In terms of frequency and cover, *Agrostis tenuis* and *Anthoxanthum odoratum* are the chief sward-forming species in nearly every unit area sampled. *Festuca rubra* var. *commutata* has a more limited distribution, but is liable to be a dominant where it does occur. The principal expression of this species appears to be under relatively heavy sheep grazing and on sandy skeletal soils. *Hypochoeris radicata* and the

indigenous *Danthonia* agg. (*D. pilosa-D. semiannularis*) rank next to these species in terms of cover, but are present in more unit areas than *Festuca rubra* var. *commutata*. The principal expression of *Hypochoeris radicata* appears to be on the skeletal soils derived from greywacke, and at the higher altitudes. *Danthonia* agg. appears to favour the steeper slopes. This taxon is usually regarded as tending to be more common on sunny faces, but the analyses made in the present work do not reflect this tendency.

The introduced species that rank among the chief subordinate species of the sward are all grasses or clovers, namely *Holcus lanatus, Lolium perenne, Cynosurus cristatus, Dactylis glomerata, Trifolium repens,* and *T. dubium*. All are widely distributed, but *Lolium perenne* and *Trifolium repens* tend to be associated more particularly with relatively heavy sheep and cattle grazing. Several introduced herbs, namely *Sagina procumbens, Cerastium glomeratum, Linum catharticum, Bellis perennis, Leontodon leysseri, Taraxacum officinale, Plantago lanceolata,* and *Prunella vulgaris,* are also widely distributed, but are less common than the introduced grasses and clovers. Most of these introduced subordinate species are perennials. Three introduced species of *Cirsium,* namely *C. vulgare, C. palustre,* and *C. arvense,* have a scattered distribution over a wide range of habitat. Such importance as they have is largely seasonal, since the first two are biennials, and the last is a dieback perennial.

The indigenous species that rank among the chief subordinate species of the sward comprise four perennial herbs and two mosses, namely *Nertera setulosa, Acaena* agg. (*A. anserinifolia-A. novaezelandiae*), *Hydrocotyle* agg. (*H. moschata-H. novaezelandiae*), *Helichrysum filicaule, Thuidium furfurosum,* and *Acrocladium auriculatum*. In general, all of these species appear to be common under both heavy and light grazing by sheep and cattle. The first five tend to be associated more particularly with the skeletal soils derived from greywacke, and with the higher altitudes, while *Acrocladium auriculatum* has a wider range. Four other indigenous perennial herbs have a more scattered distribution, but are sometimes of local importance. *Oreomyrrhis colensoi* and *Dichondra repens* appear to have much the same habitat preferences as the more common indigenous herbs, whereas *Centella uniflora* tends to be more prominent at lower altitudes. *Nertera granadensis* appears to favour shady faces and to have some association with the steep slopes between hillside stock tracks. Two indigenous mosses, *Triquetella papillata* and *Campylopus clavatus,* are fairly widespread, but are not very common.

Large monocotyledons

The principal species considered under this heading are three indigenous species of *Juncus,* namely *J. polyanthemos, J. vaginatus,* and *J. luxurians*. The first of these is among the most important non-sward-forming species. All three are more particularly species of lower altitudes, and have some tendency to be associated with sunny slopes. Further, all appear to be common under both heavy and light grazing. They show no special association with poorly drained soil. Two other large indigenous monocotyledons of some importance are *Carex lucida* and *Arundo conspicua*. *Carex lucida* appears to have much the same habitat preferences as the species of *Juncus* mentioned above. *Arundo conspicua* also tends to be a species of sunny slopes, but appears to be associated with relatively light grazing.

Ground ferns

The ground ferns of the unploughable pastures are indigenous. An important feature of these species is that they are not merely of seasonal significance. While they may die back to some extent during the winter, their occupation of any area is essentially continuous.

Pteridium esculentum and *Paesia scaberula* are the most common ferns, and also rank numerically among the most common non-sward-forming species. Although both species occur over a wide range of environment, they tend to be associated more particularly with steeper slopes, with the greywacke soils, and with relatively light sheep and cattle grazing. *Pteridum* tends to be slightly more prominent at lower altitudes, and *Paesia* at higher altitudes, while another distinction is the apparent tendency of *Paesia* to be associated with shady faces.

Next to these species in numerical importance is *Blechnum fluviatile*, which occurs in similar environments to *Paesia scaberula*, but has a stronger association with the higher altitudes. Several other indigenous species of ferns, namely *Histiopteris incisa*, *Polystichum vestitum*, *Cyclosorus pennigerus*, *Blechnum procerum*, and *B. discolor*, are less common. There is a general tendency for these species to be associated with greywacke soils, relatively light grazing, higher altitudes (particularly *Polystichum vestitum*), steeper slopes, and shady faces.

Shrubs and small trees

Indigenous species are predominant among the shrubs and small trees of unploughable pasture. The only important introduced shrub is *Ulex europaeus*, which is often plentiful at lower altitudes, particularly on steeper slopes and under relatively light grazing. Also, the introduced *Sarothamnus scoparius* occurs in localised pockets, particularly on north-facing slopes and at lower altitudes.

The most common woody species of unploughable pasture, both as a shrub and as a small tree, is *Leptospermum scoparium*. This species appears to favour the soils derived from soft sandstones and mudstones, and is much less prominent on the greywacke soils (although it appears to be advancing actively on to these soils). The presence of established plants appears to be associated with relatively light sheep and cattle grazing. At the time when the field work was carried out, the "manuka blight" disease of *Leptospermum scoparium* was not prominent in the study area, in spite of repeated efforts by farmers to spread it. Some establishment has occurred since then, but *Leptospermum scoparium* appears to be surviving, although checked or killed in places (Hamblyn 1959).

Next in numerical importance is *Coprosma rhamnoides*, which is essentially a shrubby species. It shows much the same habitat preferences as *Leptospermum scoparium*, but has a slight tendency to favour steeper slopes and shady faces. *Leucopogon fasciculatus*, another largely shrubby species, is often associated with *Coprosma rhamnoides*, but is less common.

Brachyglottis repanda and *Melicytus ramiflorus* are fairly common, both as shrubs and as small trees. They occur more particularly on the soils derived from greywacke, on steeper slopes, and under relatively light sheep and cattle grazing, and show a possible tendency to favour shady faces. The less common *Geniostoma ligustrifolium* occurs under similar conditions. The tree-ferns *Dicksonia squarrosa* and *Cyathea medullaris* are also fairly prominent under similar conditions, particularly at higher altitudes and on shady faces. Two other shrubby species of some importance are *Muehlenbeckia complexa* and *Metrosideros diffusa*, which form characteristic low dense cushions in pasture. Both species tend to favour greywacke soils and higher altitudes. The microhabitats provided by the steep slopes between hillside stock tracks and by logs and stumps appear to encourage the establishment of these two species.

The shrubs *Olearia virgata*, *O. solandri*, and *Cassinia leptophylla* are less common, although *Olearia solandri* is quite aggressive in at least one valley, and *Cassinia leptophylla* is fairly prominent at the southern extremity of the study area. *Olearia virgata* is found more particularly at higher altitudes, and the other two species at lower altitudes. All three tend to be associated with relatively light grazing.

Several other woody species become prominent towards the upper altitudinal limit of pasture. *Pseudowintera colorata* appears in pasture at about 1500 ft., and is often the most common shrub above about 1750 ft., particularly on ridge tops. *Fuchsia excorticata* tends to be prominent in similar situations to *Pseudowintera colorata*, and to replace that species in the vicinity of watercourses. Finally, there is copious regeneration of *Nothofagus fusca* at about 2000 ft. at the northern extremity of the study area.

NON-PASTURE

The non-pasture vegetation falls into two major categories, namely more or less modified forest, and "secondary growth" (Levy 1923, Croker 1953), that is, the successional vegetation that arises after forest has been cleared.

There has been little penetration of introduced species beyond the margins of the

forests, even where these forests have been modified considerably. Within the forests, a few herbaceous species, such as *Carduus tenuiflorus, Cirsium vulgare, Crepis capillaris, Hypochoeris radicata, Senecio jacobaea,* and *Digitalis purpurea,* may be found on slips, or in open places where the original vegetation has been destroyed by fire or storm.

If cleared land is abandoned, introduced herbaceous species may be common enough in the first stage of succession. However, they do not appear to survive the formation of a shrub canopy. The dominant species in the shrub and small tree stages of the succession include *Leptospermum scoparium, Brachyglottis repanda, Melicytus ramiflorus,* and *Cyathea medullaris.* The only introduced shrubs of any importance are *Ulex europaeus* and *Sarothamnus scoparius.* Both these species are characteristic of the earlier part of the shrub stage, and tend to become overshadowed, and be replaced, by the indigenous species.

DISCUSSION

PLOUGHABLE PASTURE

The great competitive vigour of *Lolium perenne* and *Trifolium repens,* under conditions of high fertility, has been recognised for a long time (Armstrong 1907), and it is even more pronounced in the case of modern high-producing strains (Levy 1951). There seems little doubt that the dominance of these two species, in combination with heavy grazing, is largely responsible for the virtual absence of indigenous species (other than species of *Juncus*) from ploughable pasture.

This conclusion is supported by the fact that indigenous weeds may be virtually absent from pasture on land that has never been cultivated, provided that *Lolium perenne* and *Trifolium repens* are the dominants. Analyses of several such pastures showed the presence, as common subordinates, of *Agrostis tenuis, Anthoxanthum odoratum,* and *Holcus lanatus,* indicating that the pastures were not of particularly high quality. Nevertheless, species other than grasses and clovers provided little cover, although a few, such as *Ranunculus repens, Cerastium glomeratum,* and *Hypochoeris radicata,* were of fairly high frequency. The only indigenous species recorded were *Juncus polyanthemos* and the moss *Triquetella papillata.* In view of the fact that even the introduced herbs, with a long history as species of grazing land, do not appear to be very common in such pastures, it is not surprising that the indigenous species are poorly represented.

Cockayne *et al.* (1932), while recognising the importance of competition in relation to the virtual absence of indigenous species from "high class" pastures, have also ascribed some significance to the usually considerable distance between such pastures and any indigenous plant-community. However, the present study has suggested that indigenous species may be scarce in pastures that are actually adjacent to a source of indigenous species, provided that those pastures are dominated by *Lolium perenne* and *Trifolium repens.*

The special status of the indigenous species of *Juncus* in ploughable pasture may be due at least in part to the rhizomatous habit, which is not common in the indigenous flora. Merry (1934) has shown that a special programme of cultivation is necessary prior to sowing, if regeneration of *Juncus* from the rhizomes is to be prevented. Further, the tough, leafless, erect stems of these species do not appear to be affected by trampling, and are rarely browsed by stock.

UNPLOUGHABLE PASTURE

The pattern of vegetation is perhaps best interpreted in terms of historical origins. On this basis, the introduced species can be treated as one group, while the indigenous species can be separated (with some borderline cases) into two groups.

The widespread occurrence of the common introduced sward-forming species is probably largely related to their presence in the original imported seeds-mixtures, while their fairly uniform distribution may reflect ability to grow under a wide range of environmental conditions. The more restricted distribution of the introduced shrubs *Ulex europaeus* and *Sarothamnus scoparius* suggests that these species are still spreading from their points of release. Both species certainly appear to be advancing in some localities.

Some of the common indigenous species of unploughable pasture are common subordinate species in the surviving forests within the warm temperate belt (0-2000 ft.). This group includes the following ferns and woody species: *Blechnum fluviatile, B. procerum, B. discolor, Histiopteris incisa, Cyclosorus pennigerus, Dicksonia squarrosa, Cyathea medullaris, Brachyglottis repanda, Melicytus ramiflorus, Geniostoma ligustrifolium, Muehlenbeckia complexa,* and *Metrosideros diffusa.* (*Polystichum vestitum, Pseudowintera colorata,* and *Fuchsia excorticata* are also common in forests in the upper part of the warm temperate belt.) Since the natural habitat of these species is characterised by reduced light and high humidity, it is not surprising that in the open they tend in general to favour the higher altitudes (which are associated with increased cloud and rain), and also the shady faces.

The other common indigenous species form a rather heterogeneous group. Firstly, there are the sward-forming species and large monocotyledons, and also *Pteridium esculentum, Paesia scaberula, Leptospermum scoparium,* and *Olearia virgata.* These are the species that appear to have been more characteristic of breaks or open places in the original vegetation. (Although its distribution within the study area may be due at least in part to deliberate spreading (Saxby 1956), *Danthonia* agg. is probably best allocated to this group.) To these should be added *Coprosma rhamnoides* and *Leucopogon fasciculatus,* which are common forest subordinates only in the well-lit *Nothofagus solandri* forests, and also *Olearia solandri* and *Cassinia leptophylla,* which may have been confined originally to the coastal vegetation. It might be expected that the members of this group would be better suited to life in the open than the members of the other indigenous group, and in general they do show some tendency to occupy a wider range of environment in unploughable pasture. In addition, some of them appear to tolerate relatively heavy grazing. It is understandable that this third group should contain some species that are generally regarded as major weeds of pasture, notably *Leptospermum scoparium, Pteridium esculentum, Paesia scaberula,* the *Juncus* species, and *Acaena* agg. As Cockayne *et al.* (1932) have indicated, the apparent aggressivenes of these species is largely due to the creation on a wide scale of habitats suitable for them.

The apparent aggressiveness of the weed species, both native and introduced, also reflects a lack of competitive vigour on the part of the introduced grasses and clovers. Because they are barriers to the establishment and maintenance of high-producing economic species, steep slopes and poor soils should probably be regarded as the two factors that are largely responsible for the present floristic composition of unploughable pasture. The influence of these factors is now being modified by the development of the aerial distribution of herbicides, seeds, and fertilisers. In view of the known effects of these practices (Matthews 1959, Suckling 1959), it is to be expected that there will be some trend towards a kind of vegetation more like ploughable pasture. However, such a trend is likely to be limited by the difficulty of achieving the same intensity and flexibility of management as on ploughable land.

Another possible change of some interest concerns the distribution of certain important or potentially important shrubby weeds, such as *Leptospermum scoparium, Ulex europaeus,* and *Cassinia leptophylla.* These are the species that do not appear to have reached their environmental limits, and may be capable of spreading considerably beyond their present range. On the other hand, their further spread may be checked by the improvement practices referred to above.

NON-PASTURE

Cockayne *et al.* (1932) have stressed that the pattern of interaction is influenced by the relative numbers of introduced and indigenous species, and by differences in life form and habitat preference. In the non-pasture vegetation of the study area, the pattern of interaction certainly appears to be related to the scarcity of woody species in the introduced flora, and also to the fact that the available introduced species are light-demanding rather than shade-tolerant. Succession in this vegetation is essentially a process of replacement of introduced species by indigenous species. This has been well demonstrated in a recent study of similar vegetation by Druce (1957).

CONCLUSION

It is evident that unploughable pasture offers the widest field for further, more detailed work on interaction. The classical studies of the effects of management on this kind of vegetation (Levy 1923, Guthrie-Smith 1926) should now be augmented by experimental studies of the effects of modern improvement practices, such as those being carried out by Suckling (1959). Apart from its botanical interest, the information obtained through such studies could well be of considerable importance in assisting farmers to make the most effective use of these new practices.

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NOMENCLATURE

The nomenclature used in the text largely follows: Allan's "Handbook of the Naturalized Flora of New Zealand"; Cheeseman's "Manual of the New Zealand Flora" (second edition) (for the indigenous phanerogams); Dobbie's "New Zealand Ferns" (fourth edition); and Sainsbury's "Handbook of the New Zealand Mosses". Deviations from the first two manuals are as follows, the displaced name being in brackets. Introduced species: *Cirsium vulgare* (*C. lanceolatum*); *Leontodon leysseri* (*L. nudicaulis*); *Sarothamnus scoparius* (*Cytisus*). Indigenous species: *Acaena anserinifolia* (*A. sanguisorbae*); *Centella uniflora* (*C. asiatica*); *Juncus luxurians* (part of *J. polyanthemos*); *Metrosideros diffusa* (*M. hypericifolia*); *Nertera granadensis* (*N. depressa*); *Oreomyrrhis colensoi* (*O. andicola*); *Pseudowintera colorata* (*Drimys*).

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APPENDIX I

SUMMARY OF RESULTS OF SURVEY

(D—dominant, C—common, o—less common)

Introduced species	Indigenous species
PLOUGHABLE PASTURE	
Lolium perenne D	
Trifolium repens D	
	Juncus polyanthemos C
	Juncus luxurians o
	Juncus vaginatus o
UNPLOUGHABLE PASTURE	
Sward-forming species	
Agrostis tenuis D	*Danthonia* agg.
Anthoxanthum odoratum D	
Festuca rubra var. *commutata* D	
Hypochoeris radicata D	
Holcus lanatus C	*Nertera setulosa* C
Lolium perenne C	*Acaena* agg. C
Cynosurus cristatus C	*Hydrocotyle* agg. C
Dactylis glomerata C	*Helichrysum filicaule* C
Trifolium repens C	*Thuidium filicaule* C
Trifolium dubium C	*Acrocladium auriculatum* C
Sagina procumbens o	*Oreomyrrhis colensoi* o
Cerastium glomeratum o	*Dichondra repens* o
Linum catharticum o	*Centella uniflora* o
Bellis perennis o	*Nertera granadensis* o
Leontodon leysseri o	*Triquetella papillata* o
Taraxacum officinale o	*Campylopus clavatus* o
Plantago lanceolata o	
Prunella vulgaris o	
Cirsium vulgare o	
Cirsium palustre o	
Cirsium arvense o	
Large monocotyledons	
	Juncus polyanthemos C
	Juncus vaginatus C
	Juncus luxurians o
	Carex lucida o
	Arundo conspicua o
Ground ferns	
	Pteridium esculentum C
	Paesia scaberula C
	Blechnum fluviatile C
	Histiopteris incisa o
	Polystichum vestitum o
	Cyclosorus pennigerus o
	Blechnum procerum o
	Blechnum discolor o
Shrubs and small trees	
Ulex europaesus C	*Leptospermum scoparium* C
	Coprosma rhamnoides C
	Brachyglottis repanda C
	Melicytus ramiflorus C
Sarothamnus scoparius o	*Leucopogon fasciculatus* o
	Geniostoma ligustrifolium o
	Dicksonia squarrosa o
	Cyathea medullaris o
	Muehlenbeckia complexa o
	Metrosideros diffusa o
	Olearia virgata o
	Olearia solandri o
	Cassinia leptophylla o
	Pseudowintera colorata o
	Fuchsia excorticata o
	Nothofagus fusca o
NON-PASTURE	
Herbs	
Carduus tenuiflorus o	
Cirsium vulgare o	
Crepis capillaris o	
Hypochoeris radicata o	
Senecio jacobaea o	
Digitalis purpurea o	
Shrubs and small trees	
	Leptospermum scoparium D
	Brachyglottis repanda D
	Melicytus ramiflorus D
	Cyathea medullaris D
Ulex europaeus C	
Sarothamnus scoparius o	