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# Twenty-five Years of Mendelian Sheep-breeding

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IN 1909 the Professor of Agriculture at Leeds exhorted me to study Mendelism, which he thought would be very important in live-stock breeding. We can understand now why it has been of less direct importance in animal production than he expected. In 1921 the Professors of Zoology and Textile Industries at Leeds set me to work on the inheritance of black in the Wensleydale breed of sheep. This served as a preliminary to the genetics of extreme hairiness in New Zealand sheep mostly of Romney origin. The Wensleydale work provided the first opportunity to devise an erroneous hypothesis in Sheep Genetics which has been followed down the years by others laid quietly to rest. At first it was thought that the facts collected from Wensleydale breeders called for a two-factor hypothesis. That was too elaborate. Black proved to be a simple recessive.

Parallel with Wensleydale breeding experiments outdoors, studies of rodent hairs indoors made me acquainted with big differences in structure between fibre types growing on the same tiny area of skin. This made it easier for attention to fasten upon the halo-hairs projecting above the rest of the birthcoat of Romney lambs born in certain planned breeding trials at Massey College in 1929. Our thinking was dominated by hairiness, and halo-hairs are very hairy fibres. They were plentiful in the offspring of parents with visibly hairy fleeces mated together, in what can scarcely now rank as breeding experiments, before the days of Lush or of benzol.

In the next few years the abundance of halo-hairs on the backs of ordinary Romney lambs was found to be strongly inherited in multifactorial fashion (Dry 1955a).

**Dominant-N and Recessive-N.**—In a search for lambs with many halo-hairs on the back a ram lamb was found in which they were of what is now called N-abundance. The name of the owner who kindly donated him begins with N—hence "N-type" This ram and his offspring and descendants were mated in various ways which demonstrated the existence of the dominant-N gene (N), for which he was heterozygous. One breeding season was, however, lost through failure to see at first that the ram had got offspring near enough to half N-type*, half not. In dealing with livestock it is not easy to remember that main genes do exist.

What proved to be the same gene appeared independently in descendants of the original mob of hairy sheep, whose birthcoats had never been seen. For two generations the sheep which evidently transmitted this gene were less than N-grade, but in the third generation the first N-grade Massey-N lamb appeared—a ram.

In the same year the first recessive-N ram was born, in a cousin mating. His parents were both grandchildren of a hairy ram bought at Feilding in 1929. Hesitation to postulate the simplest of Mendelian situations persisted, but the recessive-N gene (nr) was demonstrated without loss of time by an appropriate ratio hunt.

**Effects of the N genes.**—The dominant-N gene, N, and the recessive-N gene, nr, are spoken of as N genes.

Their effect which is central in our thinking is to make the coat of part or all of the main area—not just extremities—choc-a-bloc with halo-hairs, that is, N-grade. Halo-hairs grow in primary central follicles. In N-grade a goodly proportion of these follicles produce

**Fig. 1**

Homozygous dominant-N ram, 14 months old, carrying 10 months fleece grown following shearing as a lamb; very coarsely hairy.


**Fig. 2**

Group of N-type rams, all horned, newly shorn.

them, though it is clear that commonly some primary central follicles grow somewhat smaller birthcoat fibres. In addition, it is typical of **N**-grade to have hairy-tip-curly-tip fibres in primary lateral follicles, these fibres being coarsely hairy after birth, with some chalky medulla in the pre-natal tip (Fraser, Ross, and Wright 1954). This type is rare in non-**N**. The **N** genes boost the vigour of the primary follicles.

There is often a brown patch on the back of the lamb's neck, varying in size, which usually leaves no permanent coloration. A few brown halo-hairs are sometimes found in this position in non-**N** lambs. Sometimes brown patches, say an inch in diameter, are found elsewhere, notably to the side of the root of the tail. One or two lambs have been piebald, with large brown areas.

The fibres grown by primary follicles tend to shed freely, and they tend to be succeeded by kemps which also shed, though many successors may be persistent fibres, often coarsely hairy. The story of **N**-type kemp succession has been told by Mrs. Dawbin (Miss Janet Ross) and Mr. Graham Wright (1954). As implied already, the big birthcoat fibres which persist are usually very hairy.

There is little crimp in the coarsely hairy wool, and away from their tips the staples tend to fuse.

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* "**N**-type" includes animals less than **N**-grade, but believed to carry *one or both of the main genes,* **N** *and* **nr**, *and possessing one or more* of the several features that together characteristically make dominant-**N** and recessive-**N** sheep different from ordinary Romneys (Dry 1955b, I (a) ).


**Fig. 3**
Ewes' horns, larger and smaller.


**Fig. 4**
Ram lamb (**N**/+), aged 4 months, with two pairs of horns, one pair very small; a rare oddity.


**Fig. 5**—Large lumps bearing small scurs (N/+).


**Fig. 6**—Scurs (N/+).


**Fig. 7**—Big horns (N/N).

The **N** genes also make horns grow, unless it be that horns are determined by a second gene, closely linked. In dominant-**N** sheep horns (Figs. 1-7) are sex-influenced, dominant in rams, recessive in ewes, with a few exceptions in both sexes. Recessive-**N** rams grow horns with similarly few exceptions, but recessive-**N** ewes do not grow horns. About a quarter of carrier rams—heterozygous for the recessive-**N** gene—grow small horns.

A series of experiments started four years ago spring from the suspicion that the **N**-grade birthcoat and horns may be determined by different closely linked genes, the one for horns sex-influenced. A set of twin rams, with no halo-hairs on the back, might have received a gene for horns from their horned sire, known to be heterozygous dominant-**N** though his halo-hair back grade (III) was low-medium; their breeding performance showed these no-halo twins not to possess the gene **N**. The results of these recent experiments suggest that these twin rams received a different gene for horns, entirely independent of the dominant-**N** gene, from their ordinary Romney dam. The *indications are that this gene determines horns in sex-influenced* fashion, like **N**, i.e. that it is dominant in males, recessive in females; also, that one dose of this gene for horns-without-**N** in association with **N** in ewes, makes horns grow that are usually larger than those of any heterozygous dominant-**N** ewe that lacks this additional gene. This report, however, is tentative. The matter is being explored further. There is need for co-ordinated work on horns in sheep in a number of countries.

**Distinguishing homozygous and heterozygous dominant-N lambs.**—After a complete failure many years ago to distinguish homozygous coloured mice from coloured mice carrying the gene for albinism, the same problem was well in mind as soon as the dominant-**N** gene was discovered. Breeding tests of rams are tedious and there is no proving a ewe to be homozygous by her progeny before she is dead or very old. Hair-splitting details take you only a little way. The solution, won step by step by a team and largely due to Dr. A. S. Fraser, proved simpler and crisper than expected. With very rare exceptions, lambs with full halo-coverage over the fleece-bearing area are homozygotes (**N/N**) (Fig. 9) while lambs with some reduction below **N**-grade abundance (Fig. 8) on at least a small armpit area just behind the shoulder are heterozygotes (**N/+**).

As exceptions, about one **N**-grade heterozygote in a hundred lambs, not themselves the offspring of exceptions, has no shoulder

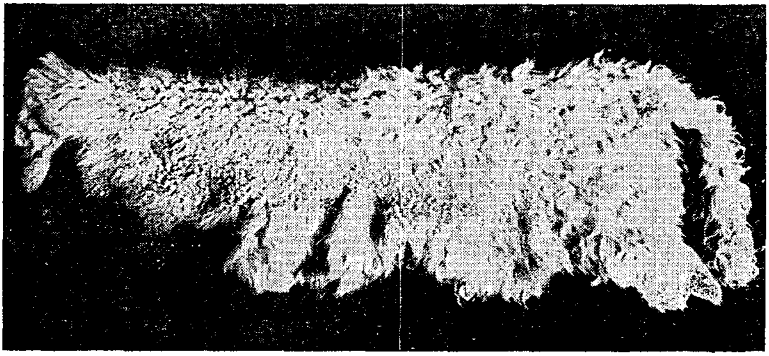

**Fig. 8**

Skin of heterozygous dominant-**N** lamb with continuous big reduction in halo-coverage at front of body and along the side.

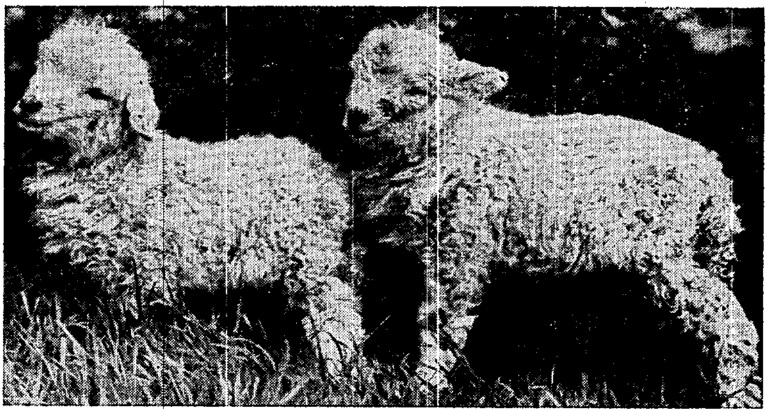

**Fig. 9**

Twin N-grade lambs with no shoulder patch, homozygous dominant-N; offspring of ewe of Fig. 10 and a homozygous dominant-N ram.

patch, and we are following up the suspicion that a very occasional homozygote has a slight reduction in halo-hair abundance in the shoulder patch region.

Horn details also help in diagnosis. A ewe with no shoulder patch that fails to grow horns is rated **N/+**, though it is possible that an odd **N/N** ewe grows only scurs. A ram lamb without a shoulder patch that lacks horn lumps at birth is judged **N/+**. Many **N/+** ram lambs are without horn lumps at birth, but many possess them, so that horn lumps are of much less significance in distinguishing the two genotypes than presence or absence of the shoulder patch.

On the average **N/N** fleeces are distinctly more coarsely hairy (Fig. 1) especially at the butt of the staple, than **N/+** fleeces and contain more kemp (Ross and Wright, 1954).

**Complications in dominant-N due to modifying factors.**—There is a hint that the growing of scurs (an inch or less), instead of horns, by **N/+** rams has a genetic basis. So certainly, have horns in **N/+** ewes, and very likely this is brought about by a main gene.

The absence of the shoulder patch in **N/+** lambs—which makes them look like homozygotes—is strongly inherited. The failure of the gene **N**, though present, to make a lamb **N**-grade—so that it is not definitely visibly different from non-**N**—has a genetic basis. (All homozygotes, as indicated earlier, are **N**-grade.) Heterozygotes less than **N**-grade may be anything from a little short (grade VI) down to no halos at all (grade I). Sheep with but few or no halo-hairs have been shown to possess the gene **N** by producing lambs of homozygous characterisation, in matings with homozygotes, in such numbers that those lambs cannot be exceptional heterozygotes (Fig 9, twin lambs of ewe of Fig 10, **N/+** grade II with non-hairy fleece). Being **N/N** they have received one dose of **N** from both parents, that is, not only from the **N/N** parent, but from the parent that looked like an ordinary Romney at birth. In these same matings many of the **N/+** lambs have been less than **N**-grade, often much less. Modifying factors are evidently hindering the expression of the gene in **N/+** parents and **N/+** offspring.

More breeding experiments are desirable on the failure of the gene N to make the birthcoat of heterozygotes N-grade. Much that is reported in recent papers has bearing on this question, but a curb must be put on speculation without more facts. It is clear that not many ordinary Romney ewes can possess a powerful load of factors that hinder the action of N in the birthcoat. In out-crosses of N/N rams to ordinary Romney ewes the percentages adopted as standard in the N/+ offspring are: 85% N-grade, 10% grade VI (the highest of the six other grades), and 5% less than VI. It is true, however, that the N/N rams have been "well bred" in the sense that in their N/+ ancestors there has been selection against factors interfering with the expression of the gene. Selection has favoured such modifying genes in several experiments, and has proved effective. Indeed, one gets the impression that the gene may have difficulty in breaking away from its inhibitors. Probably it is sometimes transmitted in Romney flocks for a series of generations without making any lambs N-grade. One would like to collect lambs with high abundance, short of N-grade, from Romney flocks, and test them. It may be remarked that if the gene N were present in a stock or breed in which the modifying factors were abundant, it could be difficult to discover that the inheritance of N-grade was anything but multifactorial.

**Recessive-N details.**—It may suffice to say that recessive-N lambs are more consistently N-grade than are heterozygous dominants. Just a few are grade VI, but it is doubtful whether any are ever of a lower grade. About one recessive-N lamb in 8—by contrast with one in 100 heterozygous dominants—has full halo-coverage. On the other hand, horns grow less well than in heterozygous dominants. They tend to be small in the rams, and the nearest approach to them in ewes has been scurs in just one animal.

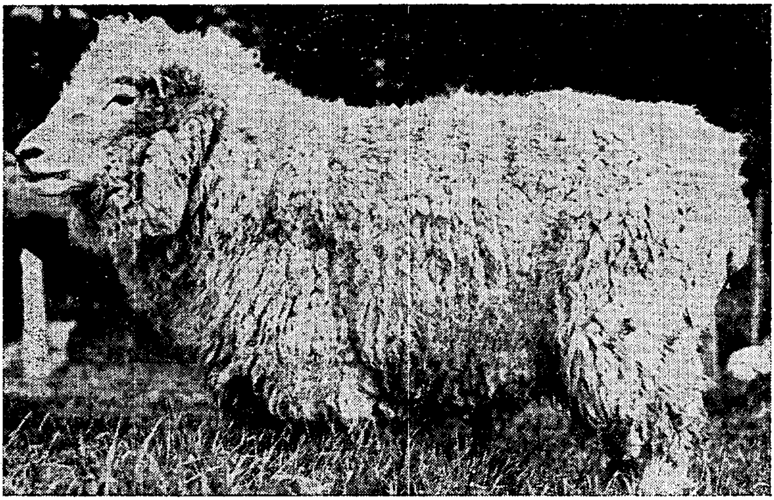

**Fig. 10**

Dam of N/N lambs of Fig. 9 by N/N ram. The birthcoat had few halo-hairs, being of grade II; the fleece was always an ordinary Romney type, not hairy. This ewe was sired by a ram considered N/N on all that is known about him. On origin the ewe is therefore deemed N/+ and this is confirmed by her producing, in different seasons, three offspring of N/N characterisation.

One dose of the recessive-**N** gene, in carriers, makes halo-hair abundance on the back higher than in ordinary Romneys. Carrier lambs more frequently have many halo-hairs (grades VI and V). This fact will be recalled later.

**Relation between the genes N and nr.**—Because the two genes produce the same effects one wonders: Are **N** and **nr** different versions of the same gene? Or does the same gene occupy different positions?

The two genes are not alleles. This was shown by the non-N lambs born in the first experiment of a series covering the years 1945 to 1955 in which for a long time it was rather difficult to decide whether the genes are linked or independent. A little later such knowledge of dosage effects as we possess will be applied in interpreting the results of those experiments.

Because the genes are not alleles the theory that dominant-N is a duplication of recessive-N, brought about by unequal crossing over, collapses. The nature of the material makes the theory of translocation with position effect, due to A. S. Fraser, difficult to disprove or establish. As country cousins of the Drosophila workers we draw freely on them in our thinking.

The rest of this sketch deals with matters in which most progress has been made in later years, by building on what was learnt earlier.

**Dosage effects.**—Because **N** and **nr** are not alleles it is possible to breed sheep that are homozygous for both. This genotype is written **N/N.nr/nr.** One would like to know: Are such animals of more extreme characterisation than those homozygous for **N,** but without **nr,** i.e. **N/N.+nr/+nr,** or to simplfy the symbols, **N/N.+/+**? On interbreeding N-type sheep produced by crossing the stocks and therefore **N/+N.+nr/nr,** or **N/+.+/nr,** the expectation is that 1/16 of the $F_2$ lambs will be homozygous on both counts, and other $F_2$ lambs which one is prepared to find of robust characterisation are the two other genotypes with two doses of **N,** namely **N/N.+/nr** (1/8), **N/N.+/+** (1/16), and it is no surprise to conclude—as will be explained shortly—that **N/+.nr/nr** is also robust.

As expected, a goodly number of $F_2$ lambs have been of homozygous dominant characterisation, and it is likely that some six or eight have been double homozygotes. Nothing has been noticed in the young animals that eclipses the early features of homozygotes of the dominant-**N** stock. One ram of those with a chance to be a double homozygote was very coarsely hairy indeed, but amongst his contemporaries of the dominant-**N** stock one ram surpassed him. It may well be that two doses of **N** by themselves can determine as extreme a Romney fleece as two doses of **N** in association with one or two doses of **nr,** though conceivably double homozygotes might average more robust fleeces than plain homozygous dominants. However, as will be explained directly, recent findings point to a slower but neater method of producing double homozygotes than by interbreeding double heterozygotes.

Very occasional heterozygous dominant-**N** sheep, taken for definite reasons to be free from **nr** (Dry 1955b, II(g) and 1955c, II(b) (vi) ), look like homozygous dominants. A very small number of heterozygous ewes have both full halo-coverage and horns. Heterozygous rams have a better chance to deceive, for horn lumps at birth are common in heterozygotes.

In two other genotypes that fall short of high gene dosage animals that are like homozygous dominants are more common, but by no means abundant. Of recessive-N's **(+/+.nr/nr)** about 1 in 8 lacks the shoulder patch, and the estimate of the frequency of rams looking like homozygous dominants is 0.07, but zero in ewes, for they have never grown horns. In double heterozygotes (N/+.+/**nr**) the estimated frequencies are 0.15 in rams, 0.10 in ewes (Dry 1955c, II(c) ).

It will be observed that two doses of **nr** obliterate the shoulder patch more often than one dose of **N**. By contrast, while about 1 in 10 **N**/+.+/+ ewes has horns, recessive-**N** ewes do not grow them.

On available information one dose of **nr** appears able to join forces with one dose of **N** in the growing of horns*, and the two in partnership give complete halo-coverage with frequency indistinguishable from that of recessive-**N** ewes (Dry 1955c, II(b) ).

By applying the estimates just quoted to an appropriate mating we can learn something, which indeed proves quite simple, about the characterisation of **N/+.nr/nr.** In the mating between double heterozygote and recessive-**N, N/+.+/nr,** × **+/+.nr/nr,** assuming the two genes to be on different chromosomes, the expectation is equal numbers of **N/+.nr/nr, N/+.+/nr, +/+.nr/nr, +/+.+/nr.**

The last named, carriers, with one dose of the recessive-**N** gene, are so far not known to be **N**-grade†. The expectation therefore is 3 **N**-types to 1 non-**N**, and in the **N**-types one-third of the only high dosage genotype which can be produced in this mating. As stated above, a few of the **N/+.+/nr** offspring of both sexes and a few of the **+/+.nr/nr** rams, will look like homozygous dominants.

In the actual matings 104 lambs were born, exactly half of each sex. The expected number of **N**-types is 78, composed of 26 of each of the three **N**-type genotypes named above. The two genotypes of lower dosages are expected, from the data now being applied, to include 4 (to the nearest whole number) with the chacterisation of homozygous dominants, and 48 like heterozygous dominants.

Examine the following figures:

| | Characterisation | | |
|---|---|---|---|
| | **Like N/N** | **Like N/+** | **Non-N** |
| Expected apart from **N/+.nr/nr** | 4 | 48 | 26 |
| Actual‡ | 28 | 49 | 27 |
| Expected if all **N/+.nr/nr** are of N/N characterisation | 30 | 48 | 26 |

Thus it is concluded that all **N/+.nr/nr** animals, or almost all, have the robust characterisation of homozygous dominant-**N's.**

This sketchily presented argument is one example of how one step has led to another as the years have rotated. Half the lambs in the mating which brings this story to its climax were born in 1955, and their begetting was very fortunate. There has been reluctance to discard rams with valuable contributions to their credit, and the only fertile double heterozygote available proved to be the ram born in 1945, who had figured the most prominently in the interbreedings of double heterozygotes. He completed his career with a score of 54 lambs from 38 recessive-**N** ewes.

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* More **N/+.+/nr** lambs are being bred from heterozygous dominant-**N** ewes themselves not possessing horns or scurs.

† See later, under "**N**-grade lambs in crosses between recessive-**N** and ordinary Romney ewes."

‡ The figures may be very slightly changed when hornedness has been examined later in the first year of 1955 lambs.

**Are N and nr independent or linked?**—In the previous section it has been assumed that the two genes reside on different chromosomes. The mating between double heterozygotes and recessive-N's has given the perfect 3 N-type : 1 non-N ratio (77 to 27) expected on independent assortment. By contrast, the interbreeding of double heterozygous expected to give the 13 : 3 ratio, has given a consistent deficiency of non-N lambs. The figures are 120 N-type : 16 non-N, instead of 110½ : 25½. $X^2$ is 3.9. If the genes entering the cross from opposite sides were on opposite members of the same pair of chromosomes, the crossover percentage would be 27.3. The 3 : 1 ratio in the back-cross might be a fluke, but it may be stated without elaboration that the figures for the three groups—homozygous dominant characterisation, heterozygous dominant characterisation, and non-N—are not likely to be due to chance. It is reasonable to believe that the genes are on different chromosomes.

**A programme for breeding double homozygotes (N/N.nr/nr).**—On interbreeding double heterozygotes, lambs of all known N-type genotypes, namely, seven, are produced. In four of these we expect all offspring (or almost all) to be of homozygous dominant characterisation, but to which of these genotypes a particular animal belongs we cannot tell by inspection on present knowledge. Most of these sheep will be homozygous for the gene N, but how many nr genes one of these possesses—2, 1 or 0—we cannot say, and it is not realistic to contemplate breeding tests.

The recent results just discussed show that a way to breed double homozygotes with a better chance of being known to be of that genotype, is to begin with the mating that has loomed large in 1955. This mating, **N/+.+/nr x +/+.nr/nr,** cannot give lambs homozygous for N, but a third of the N-type lambs are **N/+.nr/nr.** Of those like **N/N.+/+** in halo-coverage and hornedness most will be **N/+.nr/nr,** homozygous for the elusive recessive gene. Retain them, with some leaning to those with very hairy fleeces, though this preference is little more than a guess. On interbreeding animals that are really **N/+.nr/nr** a quarter of the offspring will, of course, be homozygous for both genes. How to distinguish these from animals not homozygous for the dominant gene would assuredly still be a problem. The rams could be tested for homozygosity for N down a series of generations, while material produced in the way now suggested should be used in seeking to distinguish the several genotypes without breeding tests.

**N-grade lambs in crosses between recessive-N and ordinary Romney ewes.**—In matings between recessive-N rams and ewes without halo-hairs on the back from Romney flocks, about one lamb in 25 has been N-grade. These anomalous lambs have been the object of much speculation. One proved explanation is that the no-halo ewe has transmitted a dominant-N gene. An obvious possibility is that the no-halo ewe has transmitted one dose of the recessive-N gene. In associated work that gene has been brought to the College in a no-halo ewe from the same flock as one no-halo ewe that proved to be heterozygous dominant-N. A third possibility now under investigation is that only a single dose of nr occasionally determines N-grade, without help from any main gene. This would not be surprising in view of the fact that carriers have many halo-hairs on the back more often than ordinary Romneys.

**The dominant-N gene and growth rates.**—It looks as if the dominant-N gene does something to reduce the rate of growth of lambs of all-Romney origin, especially if conditions are unfavourable. Mr. F. R. Cockrem has opened the detailed study of this problem. There is apt to be disharmony between mutant or strange genes in a genetic background not adapted to coping with them. In recent years the first consideration in the choice of rams has been good growth rate in their first year. This selection appears to have been effective, but one cannot be sure how much is due to nurture.

**The dominant-N gene in crosses.**—Crosses have been made to Lincolns and Cheviots. Homozygotes have been produced with half and with a quarter Lincoln "blood" and other homozygotes with the same two proportions of Cheviot blood. One has an eye for various comparisons. Lincolns, it might be said, are accustomed to growing coarse fibres in very heavy fleeces, and Cheviots are hardy. The wools so produced differ from Romney **N**-type in readily recognisable features.

To conclude with one forward glance, there would seem scope in planting not only the dominant-**N** but the recessive-**N** gene, not only singly, but together, into other breeds or combinations of breeds.

## REFERENCES:


Dry, F. W. (1955a)—Multifactorial inheritance of halo-hair abundance in New Zealand Romney sheep, **Aust. J. Agr. Res.** 6: 608-23.

Dry, F. W. (1955b)—The dominant **N** gene in New Zealand Romney sheep. **Aust. J. Agric. Res.** 6: 725-69.

Dry, F. W. (1955c)—The recessive **N** gene in New Zealand Romney sheep. **Aust. J. Agric. Res.** 6: 833-862.

Fraser, A. S., Ross, Janet M., and Wright, G. M. (1954)—Development of the fibre population in **N**-type sheep. **Aust. J. Agric. Res.** 5: 490-502.

Ross, Janet M., and Wright, G.M. (1954)—Kemp succession in **N**-type sheep. **Aust. J. Agric. Res.** 5: 503-10.