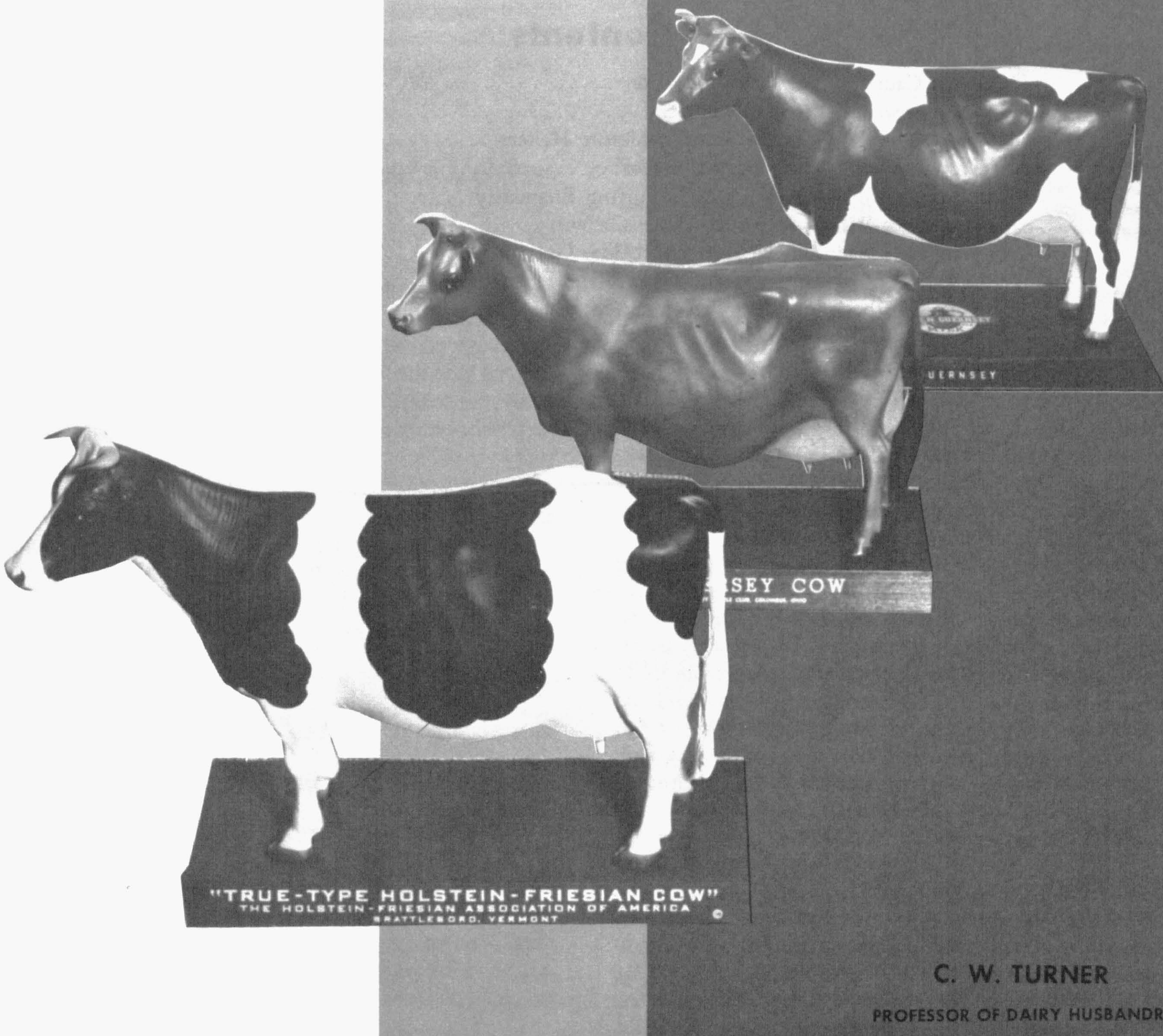
WHAT CAUSES HIGH PRODUCTION?



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Contents

WHAT CAUSES HIGH MILK PRODUCTION?

In the previous bulletin of this series (What Causes High Production?[1]) it was suggested that ***the inherited capacity of a cow for high milk and fat production is dependent to a large extent upon the inherited ability to secrete optimum amounts of a number of hormones which influence her productivity.***

It was emphasized that the most fundamental cause of differences in milk yield of individual cows is the ***size of the udder*** and especially the amount of milk secreting tissue present. The milk secreting tissue is made up of individual cells. The number of cells in the udder is determined by the secretion rate of the hormones which stimulate their growth. The present bulletin will be devoted to the story of the role endocrine-glands play in udder growth.

The Growth of the Cow's Udder

The cow's udder is composed, essentially, of two types of tissue—glandular or secretory, and connective or supporting tissue. While larger udders require more connective tissue, the essential part of the larger udder is the amount of glandular or milk secreting tissue present. When referring to udders of large size, the amount of glandular tissue is the important consideration, for it is in the cells of the glandular tissue where milk is secreted.

The udder of a calf at birth contains very little glandular tissue. It is confined to a number of ducts extending from the cistern into fatty connective tissue (Fig. 1). In sexually immature calves, the udder as a whole, and the glandular tissue, grows in proportion to the increase in body size. This is because the hormones which stimulate the growth of the glandular tissue begin to be secreted only when the calf or heifer reaches sexual maturity.

Growth of the Udder in Sexually Mature Heifers

When heifers reach sexual maturity, begin estrous cycles (heat periods), the gonadotropic hormones of the anterior pituitary gland stimulate the ovaries to follicle development and maturation of ova (eggs) (Fig. 7). Associated with this development, the ovaries begin to

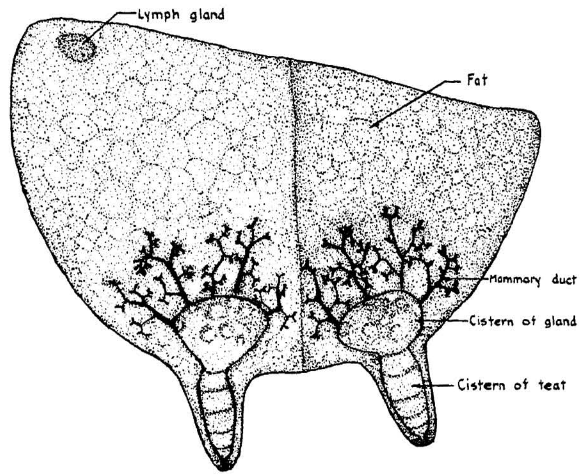

Fig. 1. The udder of an immature heifer. The udder at this time is composed of four quarters consisting of fatty tissue. The teats and cisterns of the glands are present, but the milk secreting tissue has not developed. The ducts which later carry the milk from the glands to the cistern are beginning to develop (Diagrammatic).

secrete a hormone called ***estrogen*** (female sex hormone). When ovulation occurs, the follicle quickly develops into a corpus luteum (yellow body) which secretes a second ovarian hormone called ***progesterone.***

With each recurring estrous cycle, the glandular tissue is stimulated to rapid growth. At this time, the glandular tissue consists of ducts which grow from the cistern of each quarter of the udder upward into the fatty tissue. After heifers have passed through a number of estrous cycles, the ducts show much branching and have extended into the udder to variable degrees (Fig. 2 and 3).

If heifers are not bred or do not conceive until two or three years of age, the stimulus of the hormones secreted at each estrous cycle may stimulate varying degrees of lobule-alveolar development comparable to that stimulated during early pregnancy. Thus, while duct development is the first stage of mammary gland growth, as duct growth is completed, the second stage of gland development, lobule-alveolar growth, begins. In heifers in which the hormonal stimulus for gland growth is great, the more extensive will be the total amount of milk secreting tissue present.

Evidence for the belief that increasing lobule-alveolar growth occurs during recurring estrous cycles has been obtained by stimulating virgin dairy heifers of increasing age to secrete milk by the use of estradiol benzoate at the rate of 0.3 mg/100 lbs. body weight/day for 14 days. Milking began immediately and continued until the heifers reached maximum milk production. The highest daily milk yield for a period of one week was considered

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[1]**University of Missouri Agriculture Experiment Station Bulletin 795.**

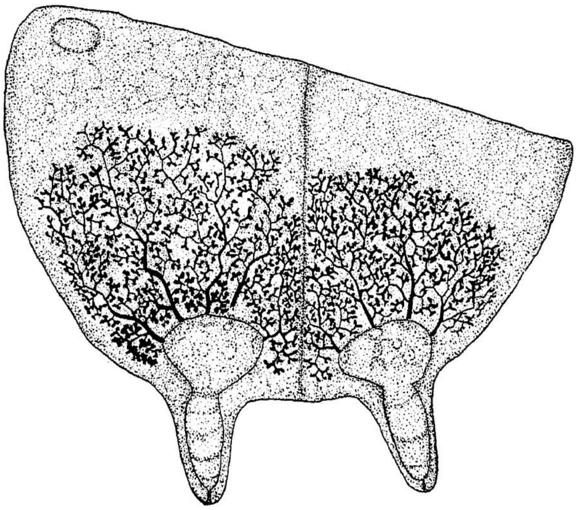

Fig. 2. The duct system begins to grow into the fatty pad contained in each quarter of the udder when heifers reach sexual maturity. After heifers have passed through a number of estrous cycles (heat periods), the ducts will show much branching and the beginning of lobule-alveolar development comparable to that stimulated during early pregnancy. If heifers are not bred until 2 or 3 years of age, the amount of glandular tissue capable of milk secretion will become extensive in heifers with considerable potential milk secreting capacity (Diagrammatic).

Fig. 3. A section of an udder of a sexually mature heifer shows the growth of the duct system and early lobule-alveolar development in the front and rear quarters. It will be noted that the udder still contains much fatty tissue into which the duct and lobule-alveolar systems have not yet penetrated.

to represent the extent of lobule-alveolar development. While milk ducts are capable of limited milk secretion, it is considered that the amounts of milk obtained from most of the heifers could not have been produced by ducts.

In two immature heifers (7 and 8 mo. old), it will be noted that milk secretion was very limited (Table 1). In a group of 5 yearling heifers (11 to 13 mo. old), the mean maximum daily milk yield was 10.0 lbs. In the group of 7 heifers 1½ years old, their mean production was only 7.0 lbs. As will be noted there were two heifers of very low production. Again, in the group of 9 heifers 2 years of age, there was considerable individual variation with a mean of 12.5 lbs/day. However, two heifers produced over 20 lbs.

Milk secretion was initiated experimentally, also, in a group of 8 heifers 3 years of age. Their mean production was 12.6 lbs. Since the mean milk production of the 2 and 3 year old heifers was similar, it may indicate that little additional growth of the udder can be induced after 2 years of age.

Ten of the heifers were again administered estradiol benzoate at the same levl for 7 days starting when the heifers had been in lactation for 45 days. At the beginning of the second course of injections, the mean maximum milk yield was 12.7 lbs./day whereas following restimulation their mean production increased to 24.5 lbs./day, an increase of 92.9%. Four heifers given a third course of injections of estrogen after 15 weeks of lactation were stimulated to secrete 22.4% more milk. A possible explanation for the marked increase in milk yield by the second injection will be discussed later.

No one has suggested previously that lobule-alveolar growth occurred in heifers before pregnancy. In laboratory animals, only duct growth has been observed up to the time of pregnancy. The considerable amounts of milk which can be stimulated by estrogen administered for only 2 weeks could not possibly be produced by a duct system. The lobule-alveolar growth induced by recurring estrous cycles in dairy cattle is believed to be caused by th longer cycle (20 days) in cattle as compared to the 4 to 6 day cycle in rats and mice. Estrogen and progesterone are probably secreted for 16 to 18 days of the cycle before the next follicle develops.

Growth of the Udder During Pregnancy

When heifers are bred for the first time, growth of the udder is continued at a more rapid rate because the hormones now act continuously instead of cyclicly during the recurrence of estrus. If the heifers have passed through only a few estrous cycles, the initial growth will consist of an extension of the duct system to the upper parts of the udder. Numerous side branches form also. In more mature heifers in which duct growth nears completion, the growth of the lobule-alveolar system is started or continued. At the sides or ends of the smaller ducts, many small branches form clusters of tiny spherical compact end-buds called alveoli. Each alveolus is lined with cells facing a central cavity called the lumen. Each cell is capable of secreting milk into the lumen. However, during the early period of alveolar growth, the lumen is inconspicous containing no milk (Figs. 4 and 5).

Surrounding groups of alveoli, a delicate connective tissue membrane is formed (Fig. 6). A group of alveoli

Table 1. Milk Yield of Heifers of Increasing Age Stimulated by Estrogenic Hormone

Herd No.	Age Mo.	Mean Milk Production/Day During Week of Maximum Production					
		Initial Stimulation 14 days		Second Stimulation 7 days after 45 days		Thyroid Stimulation 7 days after 105 days	
		Body Wt. lbs	Milk Yield lbs	Body Wt. lbs	Milk Yield lbs	Body Wt. lbs	Milk Yield lbs
G19	8	450	0.2				
H20	7	600	0.5				
Ave.			0.35				
H30	12	700	9.4	755	18.7		
H23*	13	850	10.4				
H24*	13	760	12.5				
H25*	12	670	7.7				
H26*	11	670	9.9				
Ave.			10.0				
H27	18	766	9.7	900	19.7		
H28	18	755	15.2	900	28.0		
H29	18	640	6.2	820	23.5		
G18	18	770	2.5	950	4.7		
G891	18	800	4.0				
G413	18	750	2.2				
G29	18	700	9.4				
Ave.			7.0				
H31	24	1027	25.0	1150	35.0		
H32	24	1140	21.9	1315	30.8		
BS16	24	1000	14.0	1200	24.5	1300	29.2
BS17	24	995	12.8	1150	21.7	1300	28.8
Ave.					28.0		29.0
G268	24	980	9.6				
G274	24	1000	7.5				
G411	24	800	11.8				
G270	24	940	1.0				
H26	24	1500	8.5				
Ave.			12.5				
H11	36	1560	9.8	1640	38.1	1740	43.9
J647	36		15.5				
J649	36		13.9				
H891	36		13.2				
J412	36		9.9				
J413	36		18.7				
J401	36		8.2				
J411	36		11.4				
Mean			12.6				

is called a lobule. Many lobules, in turn, are bound together by a thicker membrane to form lobes. Supporting the entire glandular mass are sheets of connective tissue which are attached on either side of the quarters. Thus, the milk secreting tissue is separated and supported throughout the quarter by connective tissue.

The milk secreted by the cells of the alveoli pass through ducts of increasing size and eventually lead into the cistern at the base of the teat. These ducts penetrate the connective tissue membranes within each quarter of the udder.

On the basis of histological study of the alveoli in heifers during the first pregnacy, the growth phase was observed to continue during the first 5 to 6 months (Fig. 7). Following this period, the epithelial cells lining the alveoli and duct system gradually begin to function. During this period, it is difficult to observe the growth process histologically. It has been assumed that when lactation was initiated the growth of additional cells gradually stopped. Recently, in experimental animals (rats and mice), a new method of measuring the growth (See p. 23) of mammary gland cells has been developed. It

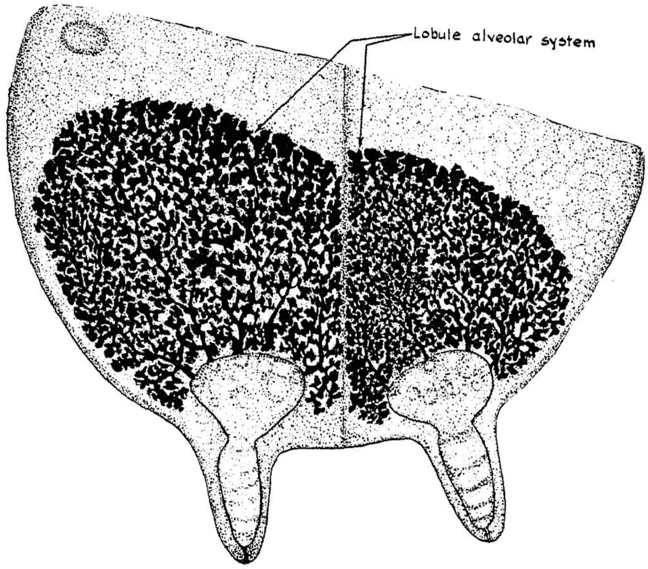

Fig. 4. When a heifer becomes pregnant, growth of the duct and lobule-alveolar systems continue uninterrupted. This growth phase continues throughout pregnancy. The development of millions of alveoli is of great importance because the cells lining the alveoli secrete milk. The amount of milk which a cow is capable of producing at the peak of production is primarily dependent upon the number of alveoli present in the udder.

This figure shows the extent of the growth of the lobule-alveolar system at about the sixth month of pregnancy when milk secretion has not yet begun in a first calf heifer (Diagrammatic). There is continued growth into the fatty tissue during the last three months of pregnancy and during early lactation.

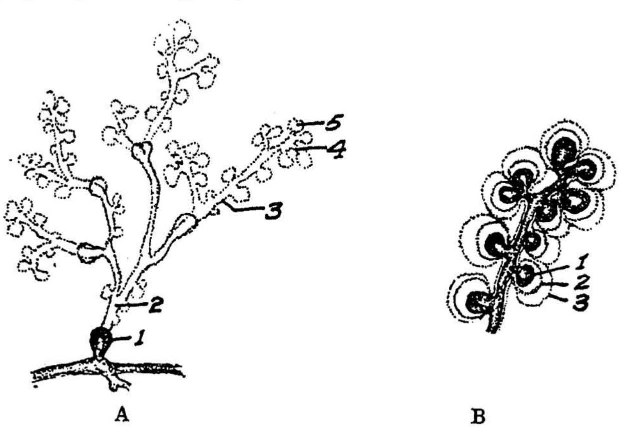

Fig. 5. (A) Drawing shows the growth of a single duct and its gradual transformation into a section of a lobule-alveolar system: 1, The branching of the duct system begins as bud-like outgrowths from the cells of the ducts; 2, The bud forms a branch of the duct; 3, Further branches then form either at the end or sides of the duct; 4, Finally, at the side and ends of the ducts alveoli form, which are spherical, balloon-like structures with a hollow interior. The cells lining the interior of the alveoli secrete milk. The growth of the ducts and the lobule-alveolar systems begins during recurring estrous cycles and continues throughout pregnancy.

(B) When the growth of the alveoli is completed they consist of compact groups of cells. The cells lining the alveoli have not yet begun to secrete milk and do not show their balloon-like form. During the last three months of pregnancy, the cells begin to secrete milk which is discharged into the cavity called the lumen. As the colostrum or first milk accumulates in the alveolus it gradually enlarges and shows its balloon-like appearance.

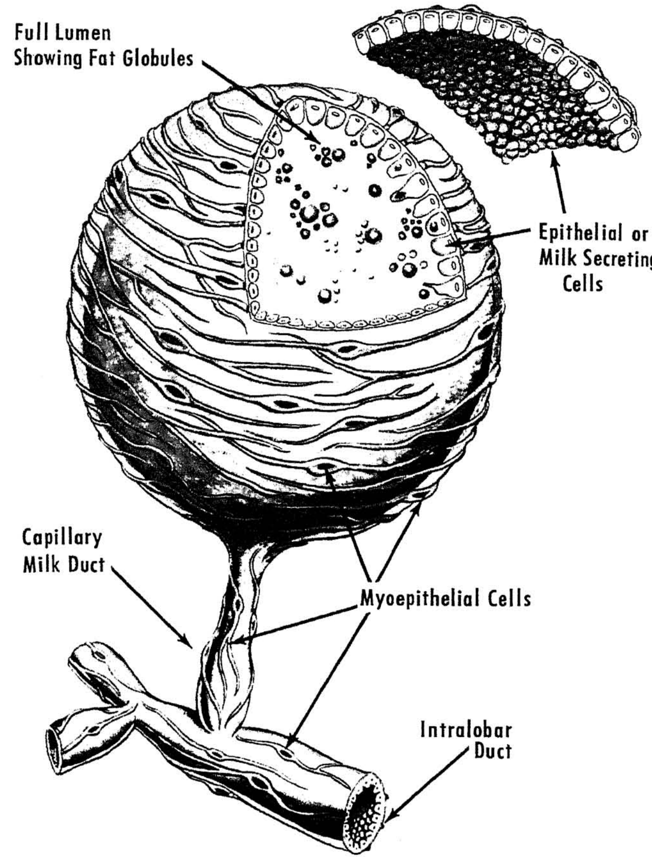

Fig. 6. The secretion of milk occurs in the epithelial cells lining the interior surface of the alveolus. The milk manufactured by each cell is discharged into the lumen or central cavity of the alveolus causing it to fill or balloon out. There are great variations in the total number of alveoli grown during pregnancy in individual cows. When the total number of alveoli is small, the maximum amount of milk produced by the cow is limited even though the hormones influencing the intensity of milk secretion may be optimal. The number of alveoli grown during pregnancy is dependent upon the amount and proportions of the two ovarian hormones, estrogen and progesterone, secreted during pregnancy.

has been shown by this method that growth of the milk secreting cells continues during the entire period of pregnancy and into early lactation. It is believed that these observations apply also to the growth of the cow's udder.

During the first 5 or 6 months of pregnancy, the growth of the lobule-alveolar system is not evident externally. The growth of the ducts and alveoli into the fatty content of the udder simply replaces the fat present.

After the sixth month of pregnancy, the epithelial cells lined the alveoli and duct system gradually begin to function. The colostrum or first milk secreted by the cells passes out into the lumen of the alveolus and into the duct system. This causes the individual alveoli to balloon out and the heifer's udder enlarges. The rate of colostrum secretion is slow at first, but increases toward the end of pregnancy. If heifers are milked during the last 2 to 3 weeks before calving, a gradual increase in

ENDOCRINE CONTROL OF UDDER GROWTH

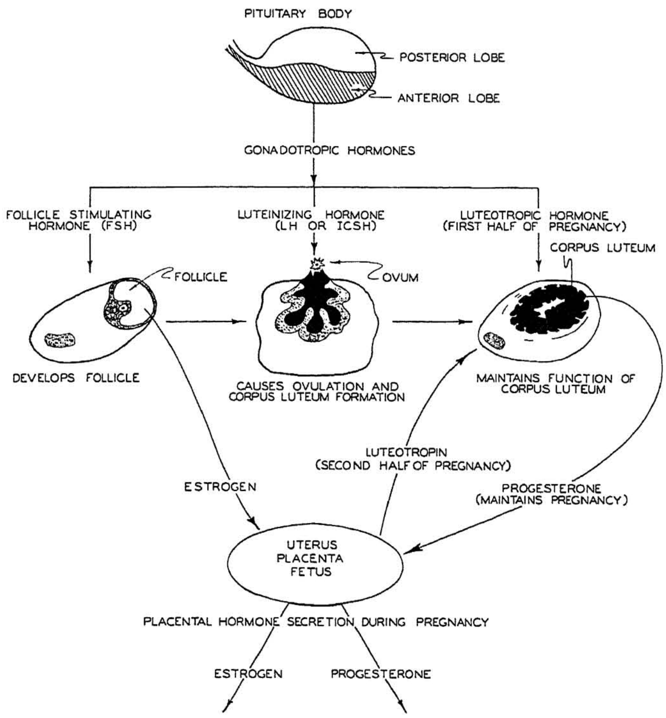

Fig. 7. The pituitary secretes gonadotropic hormones which act upon the ovary to stimulate the estrus cycle. First, the follicle stimulating hormone (FSH) causes the ovarian follicle to develop. At this time estrogen is secreted which acts upon the duct system of the udder. In addition, the egg or ovum is caused to mature. Then the luteinizing hormone (LH) is discharged from the pituitary to cause ovulation (discharge of the ovum) and the formation of the corpus luteum. If the animal becomes pregnant, a third hormone called the luteotropic hormone is secreted which maintains the functional activity of the corpus luteum and the secretion of progesterone during the first half of pregnancy. Progesterone prepares the uterus for the reception of the fertilized egg and maintains the growing embryo and fetus in the uterus. During pregnancy, the placenta secretes estrogen and progesterone which stimulates the growth of the lobule-alveolar system of the udder.

secretion may be demonstrated. Normally, heifers are not milked and this milk accumulates in the udder causing distention and sometimes marked congestion of the udder.

In first-calf heifers, the development of the udder during pregnancy in preparation for lactation involves two steps, growth and initiation of milk secretion. The growth phase is now believed to continue throughout pregnancy and into early lactation. The cells grown during pregnancy gradually begin to secrete milk during the last three months of pregnancy. Because the size of the udder increases only during the secretory phase, many people have had the mistaken idea that the most rapid growth of the mammary glands occurred at this time. While it is now believed that udder growth continues during the period of the initiation of milk secretion, growth is actually very rapid throughout pregnancy and during early lactation.

Increased Udder Growth with Recurring Pregnancy

In cows which calve at yearly intervals, pregnancy is initiated within 90 days after calving. Thus, the stimulus for further udder growth is initiated by the hormones of pregnancy. The extent of additional growth can be measured in part by the increase in milk production during the second lactation. However, increased production may be due in part to increased body weight. It is believed that the major part of the increase in milk production is caused by the increase in glandular tissue rather than in body weight.

Cows normally show increasing milk production for the first five pregnancies or until 7 or 8 years of age, then milk yield gradually declines. It is suggested that the gradual decline in the secretion of hormones is responsible for the decline in udder growth and milk secretion in older cows.

Hormones Which Stimulate Udder Growth

In experimental animals which have been ovariectomized, two hormones of the ovary have been shown to stimulate duct and lobule-alveolar growth. Duct growth can be stimulated by the use of the estrongenic hormone, while lobule-alveolar growth requires the use of both estrogen and a second ovarian hormone called progesterone. In cattle, these two hormones are produced by the ovaries during each estrous or heat cycle. These two hormones are believed to stimulate duct growth and lobule-alveolar growth as these cycles recur in unbred heifers. However, this growth is cyclic since these hormones are not secreted continuously.

When heifers are bred these same two hormones (estrogen and progesterone) are first secreted by the ovaries and then as the fetal membranes (placenta) are developed, these hormones are secreted in increased amounts by the placenta. These hormones are secreted continously during most of pregnancy and thus stimulate the growth of the lobule-alveolar system.

That these two hormones stimulate udder growth has been shown by their injection into a number of unbred heifers. Details of this research work has been published (Turner, 1959, Williams and Turner, 1961). The evidence is conclusive that lobule-alveolar growth during pregnancy is primarily controlled by these two hormones.

Why Do Cows Vary in Extent of Udder Growth?

Since estrogen and progesterone are believed to be the stimulators of udder growth during pregnancy the question may be asked, why do cows differ in the amount of udder tissue developed during pregnancy?

Unfortunately, not all of the reasons for the variation in the extent of udder growth are yet known. Research up to this time suggest some of the causes.

While all pregnant cows secrete estrogen and progesterone, the amount of each hormone secreted during pregnancy may vary significantly. Cows differ in the rate of secretion of these two hormones. For optimal lobule-alveolar growth, the amounts of these two hormones must be in the proper proportions. If the amount of estrogen secreted is limited or in excess, the amount of growth will be influenced. Similarly, the amount of progesterone secreted may limit udder growth. This fact has been shown experimentally by varying the levels of these two hormones in studies with rats and mice.

Response of Mammary Gland Cells to the Hormones

The cells of the animal body have been shown to vary in their response to hormones. This has been shown by the effect of increasing amounts of hormone. A few animals will respond to low levels, and more and more respond as the amount of hormone is increased. Thus, the mammary cells of some animals may divide and multiply more rapidly than in other animals to given levels of these two hormones. This could account for differences in udder size even when the same amount of these two hormones were secreted. The reason that this factor cannot be evaluated at this time will be explained in the following discussion.

Role of Other Hormones in Udder Growth

While estrogen and progesterone are believed to be the primary hormones stimulating udder growth, a number of other hormones may influence the rate of cell multiplication and total lobule-alveolar growth.

One such hormone, thyroxine, has been shown to stimulate increased size of the glands. When thyroxine was injected into either normal pregnant rats or to ovariectomized rats to which estrogen and progesterone were administered, the average amount of gland growth was increased about 25% (Moon and Turner 1960, Griffith and Turner 1961). Thus, normal animals with higher thyroxine secretion rates might be expected to respond by increased gland growth in comparison to those with lower thyroxine secretion rates. In lactating cows fed thyroprotein during pregnancy one should expect the thyroxine to stimulate larger udder size and more milk secreting cells would be available to secrete milk at the next lactation.

Similarly, growth hormone has been injected into both pregnant and experimental rats. While these animals showed slightly improved size of the mammary glands, the increase was not significant. When growth hormone and thyroxine were administered together, gland growth was increased above that stimulated by thyroxine alone. Thus, these two hormones may influence udder growth. The influence of other hormones in their ability to stimulate mammary gland growth is being studied.

It is thus possible that the variation in response of individual animals to the same amount of estrogen and progesterone may be due to variation in the secretion rates of other hormones, rather than to variation in capacity of cells to multiply.

Mammary Gland Growth in the Rat

Information on the growth of the udder of dairy cattle presented in this bulletin has been obtained during the course of many years of research. This work was guided by research conducted on small experimental animals, primarily with the laboratory rat. Rats have mammary glands comparable in structure to the cow which grow during pregnancy and lactate after parturition. The mammary glands of rats respond to various hormones quite similar to the response obtained with heifers. However, large numbers of rats can be included in each experiment to avoid individual variability and hormones can be tested which are too expensive to use with cattle.

Some years ago, it was observed that a substance called desoxyribonucleic acid or DNA is present in relatively constant amounts in the nucleus of each cell. When a cell divides into two cells the DNA also doubles. Thus, the estimation of the DNA in the mammary glands of rats offered an excellent method of measuring cell multiplication or growth. It also measures the number of cells which have been grown during stages of pregnancy and lactation.

Lactational Growth of the Udder

In studies with rats using DNA as a measure of mammary gland growth, two important discoveries were made. First, it was shown that gland growth continued throughout pregnancy in spite of the fact that the cells begin to secrete milk during the last ⅓ of pregnancy. Second, it was shown that very rapid additional growth of the mammary glands occurred during early lactation. This observation was surprising, for it had been believed that lactating cells would no longer grow or divide. It is possible that not all cells begin to secrete milk at parturition and it is these cells which may continue to multiply during early lactation.

Milk yield increases gradually during early lactation. The increased yield of milk for 30 to 60 days following calving may be caused, in part, by the growth of additional cells at this time which then begin to secrete milk.

That lactational growth of the mammary gland is not caused by the ovarian hormones has been shown by two types of experiments. First, the injection of estrogen and progesterone for periods beyond 20 days in the rat will not stimulate continued growth. Second, lactating rats may be ovariectomized immediately after parturition and lactational growth will still occur.

It has been suggested that lactational growth is stimuated by hormones secreted by the anterior pituitary and its target endocrine glands. These would include the lactogenic and growth hormones directly and thyrotropin which would stimulate increased thyroxine secretion and adrenocorticotropin which would stimulate the hormones of the adrenal cortex.

In studies in rats, the growth hormone and adrenal hormones have been shown to stimulate lactational growth. Thyroxine and other hormones may be involved.

It was shown in our laboratory some years ago that the stimulus of milking causes the discharge from the anterior pituitary of the lactogenic hormone which stimulates milk secretion. Evidence is increasing that the stimulus of milking also causes the discharge of other pituitary hormones including growth hormone, thyrotropic hormone and the adrenocorticotropic hormone. The regular discharge of these hormones would increase their secretion rates and thus stimulate lactational growth of the udder as well as to stimulate increased milk secretion.

It was shown earlier that estrogen injected would stimulate milk secretion in virgin heifers of increasing age. These heifers were milked regularly for 7 weeks. It is believed that during this period the hormones of the pituitary stimulated lactational growth of the udder for upon restimulation of lactation with estrogen, milk yield increased about 90% above the initial maximum yield (See Table 1).

Regression or Involution of the Udder

After dairy cows reach maximum milk yield after parturition, there is a gradual decline in milk production until the animals go dry. The gradual reduction in milk production may be caused in part by a slow decline in the secretion rates of the various hormones, but it is suggested that it may also be caused, in part, by a gradual loss of secreting cells into the milk.

When lactating cows are rebred at about 90 days after calving (so they will calve again within a year), there is a renewed stimulus of the hormones of pregnancy to stimulate the growth of additional cells. Apparently these new cells do not secrete milk during that lactation since milk secretion continues to decline during pregnancy. They only show their presence after the next calving period when milk yield reaches a higher level. It is believed that there is slight additional growth of secreting cells during each pregnancy until cows reach 7 or 8 years of age. This is shown by the increase in yearly milk production up to that age. If lactating cows are not rebred before they dry up, there is a loss of secreting cells stimulated during pregnancy and early lactation. However, if such cows have regular heat periods, complete loss of the lobule-alveolar system of the udder will not occur. The estrogen and progesterone secreted during each estrous cycle will preserve the extent of growth induced by the estrous cycles previous to pregnancy. In cows with a dry period between pregnancies, it is questionable whether renewed growth of the udder will equal that induced in cows which are rebred during early lactation. Thus, rebreeding cows at about 90 days of lactation should tend to maintain cows at their potential peak of lactation after each succeeding pregnancy.

Summary

Every dairyman recognizes that heifers of the same body weight differ greatly in the size of their udders. The potential milk producing capacity of the animal is dependent in part upon the size of the udder and the number of milk secreting cells present. Why do cows differ so greatly in the inherited size of the udder? Since udder growth is dependent upon the secretion of a number of hormones which have been described, it is suggested that udder size is dependent upon the inherited ability of the endocrine glands to secrete optimum amounts of the hormones which directly and indirectly stimulate udder growth.

Udder growth which occurs during recurring estrous cycles and pregnancy is primarily dependent upon estrogen and progesterone which is secreted by the ovaries and by the placenta during pregnancy. The amounts and ratios of these two hormones influence the extent of milk secreting cell growth. In addition, thyroxine from the thyroid gland and growth hormone from the anterior pituitary influence gland growth. Other hormones not yet studied may also influence gland growth.

It has now been shown that additional growth of milk secreting cells occurs during early lactation. This growth is not caused by the ovarian hormones, estrogen

and proesterone, but is stimulated by hormones of the anterior pituitary directly and by endocrine glands which they stimulate, including the thyroid gland and thyroxine, and the adrenal glands and their hormones. Thus, total mammary gland growth is dependent upon a number of hormones which must be secreted in optimal amounts to stimulate udders of large size. To the extent that one or more of these hormones are deficient the udder size will be reduced.

The Estrogenic Hormones

The estrogenic hormone is secreted in the cow's ovary. It is present in the fluid of the ovarian follicle. It flows into the blood stream and causes the cow to show the symptoms of heat or estrus at which time the cow will accept the bull.

The estrogenic hormone is of importance in the reproductive process in stimulating the growth of cells of the vagina, relaxes the uterine cervix and aids in the preparation of the reproductive tract for the reception of the ovum (egg).

Estrogens also stimulate the growth of the duct system of the udder. Cows vary in the amount of hormone secreted. If small amounts are secreted, it may not be sufficient to cause the cow to show signs of heat and the growth of the duct system may be slight.

The estrogen secreted by the ovary is called ***estradiol.*** There are also a number of other natural estrogens. The natural estrogens have been purified and their composition determined. They are included in a group of compounds called steroids. These compounds can be synthesized and are now available for use in domestic animals.

When cows become pregnant, the placenta or fetal membranes secrete increasing amounts of estrogen and become the chief source of the hormone during pregnancy.

Another group of compounds having estrogenic activity, but not produced in the body, have been synthesized by chemists. They differ from the natural estrogens chemically as shown by their structural formula. The more commonly used compounds are called diethylstilbestrol and hexestrol. They are very effective when fed and serve as a cheap substitute for the ovarian estrogen.

A second ovarian hormone, produced by the corpus luteum or yellow body, is called ***progesterone.*** The corpus luteum forms in the ovary at the site of the ovarian follicle after the ovum is discharged. It secretes progesterone for about 16 days during an estrus cycle, but if pregnancy ensues the corpus luteum is maintained throughout pregnancy and progesterone is secreted continuously.

The primary function of progesterone is to continue the preparation of the uterus (started by estrogen) for the nourishment of the fertilized egg until the fetal membranes become established so that maternal blood may be utilized. It is then required continuously during pregnancy to maintain the connection of the maternal and fetal membranes. If the corpus luteum is removed and progesterone is no longer secreted, then abortion quickly occurs.

The second important function of progesterone is to stimulate the growth of the lobule-alveolar system of the cow's udder in conjunction with estrogen.* While progesterone from the corpus luteum is the chief source of supply in early pregnancy, later, the placenta (or afterbirth) also secretes progesterone to supplement the supply.

The structural formula of progesterone indicates that it is similar to the estrogens in being a steroid. It can be synthesized by chemists and is available for use in domestic animals. A number of related compounds have been shown to have physiological actions similar to progesterone but are secreted in the animal body only in small amounts.

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