THE RATE OF GROWTH OF THE DAIRY COW.

IV. GROWTH AND SENESCENCE AS MEASURED BY THE RISE AND FALL OF MILK SECRETION WITH AGE.

BY SAMUEL BRODY, ARTHUR C. RAGSDALE, AND CHARLES W. TURNER.

(From the Department of Dairy Husbandry, University of Missouri, Columbia.)

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The increase of milk secretion and body weight in the dairy cow follows exactly the same course from the age when milk secretion usually begins (2 years), to the age when maximum body weight is reached (about 8 years).[1] It is therefore concluded that the increase of milk secretion with age may be used as a measure of growth in the same sense that the increase of body weight with age is used as a measure of growth. After the age of maximum body weight is reached, it remains practically constant and can therefore no longer be used to measure the effect of age on the condition of the body; but milk secretion takes a downward course after passing the age of maximum body weight and steadily declines with age. This steady decline of milk secretion with age suggests the possibility of using milk secretion as a measure of the effect of age on the body after age ceases to have an appreciable effect on body weight—in other words, to use the declining curve of milk secretion as a measure of senescence. In the absence of contradictory evidence, there seems no reason to believe why the course of milk secretion which was found to be a good quantitative measure of growth during the growing phase of life, should not also be a good quantitative measure of senescence during the declining phase of life. Adopting the point of view that the rising and falling curve of milk secretion with age is a representation of developing and declining physical powers with age due to the processes classed under growth and senescence, we have brought together a large amount of data on the change of milk secretion with

[1] Brody, S., Ragsdale, A. C., and Turner, C. W., *J. Gen. Physiol.*, 1923–24, vi, 21.

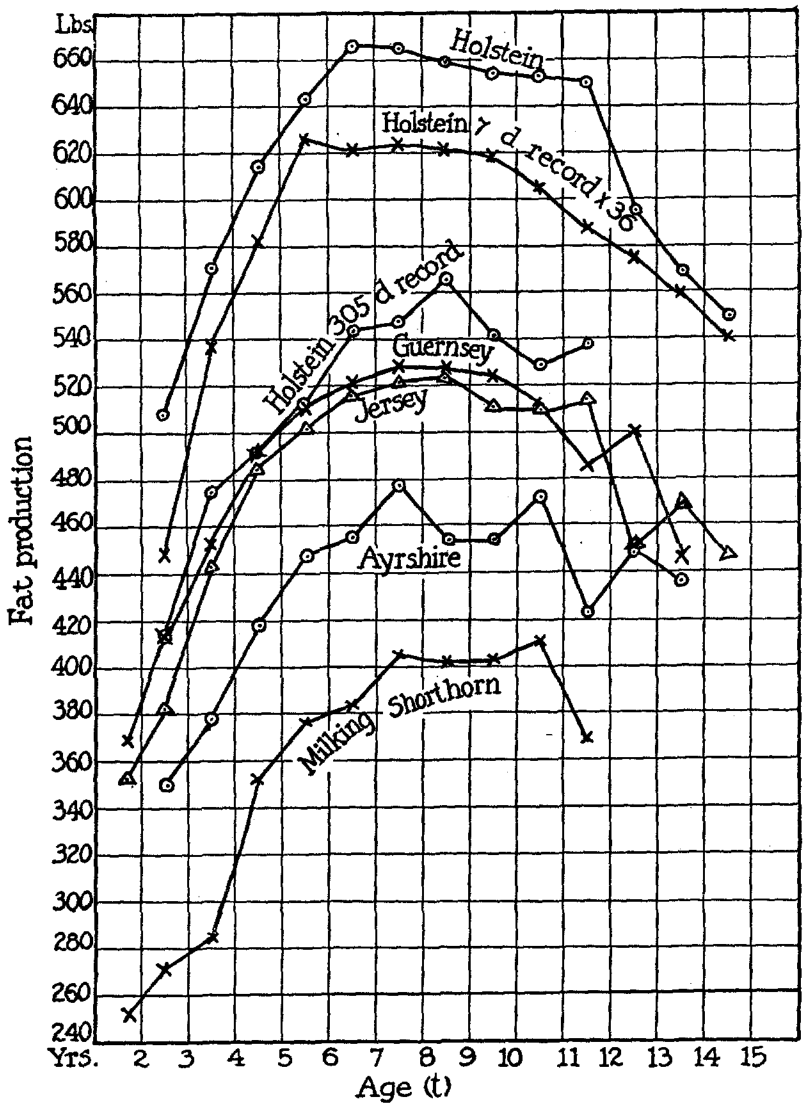

FIG. 1. The course of milk secretion with age for several breeds of dairy cattle plotted from data in Table I. With the exceptions noted on the curves, the curves represent the butter fat production per year of 365 days. For the Guernsey cows, the records represent 365 days or less, if the cow happened to dry off before the end of the year. The curves in this figure represent a total of 150,544 records.

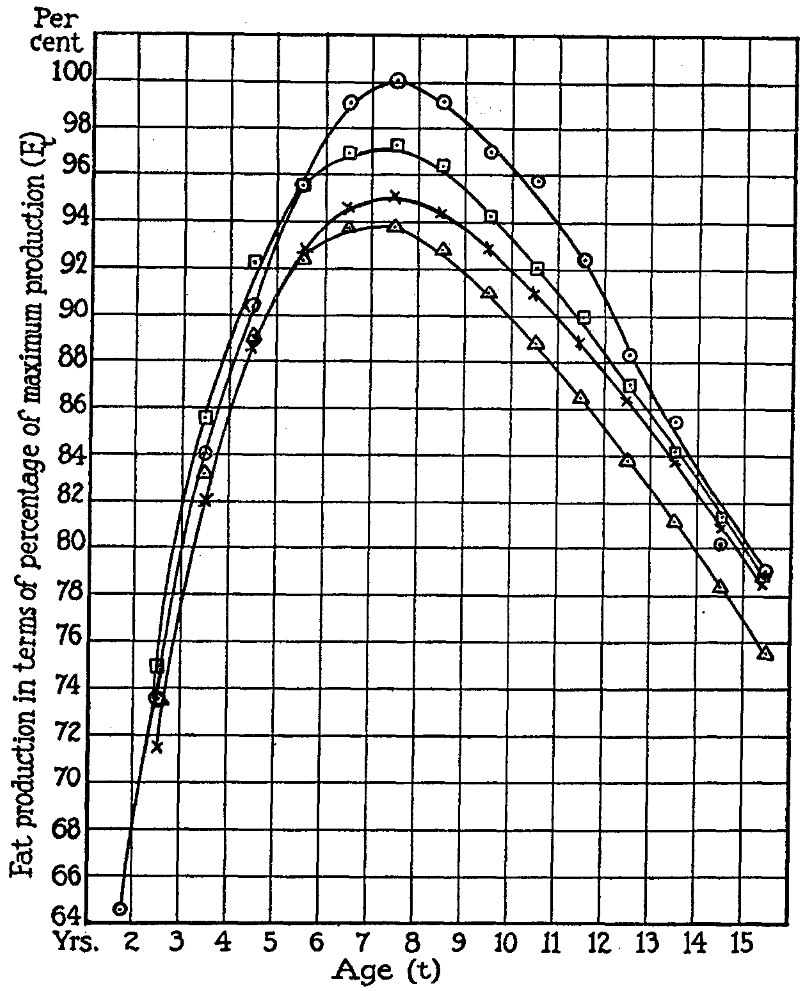

FIG. 2. Comparison between computed and observed values of milk secretion with age for yearly records. The circles represent observed values of the weighted averages of all cows yearly and 305 day records expressed as percentage of maximum production given in table I. The other values were obtained from trial equations as follows: ⊡ represents $F_t = 142.4e^{-0.377t} - 126.15e^{-0.331t}$; + represents $F_t = 142.4e^{-0.0377t} - 126.15^{-0.310t}$; △ represents $F_t = 142.4e^{-0.04t} - 120e^{-0.310t}$. After the age of 12 years, the observed values are not reliable due to the small number of animals represented. The observed values in this figure are based upon 45,984 yearly and 10 monthly records.

age for the purpose of presenting a continuous quantitative picture of the two phases of life, and, if possible, to formulate a rational theory of the quantitative changes of the physical powers during growth and senescence.

Figs. 1, 2, and 3 plotted from data in Table I show the rise and fall of milk secretion with age from 2 years, the age when milking usually begins, until 14 years. These curves represent, of course, only a portion of the picture of rising and falling physiological activities of

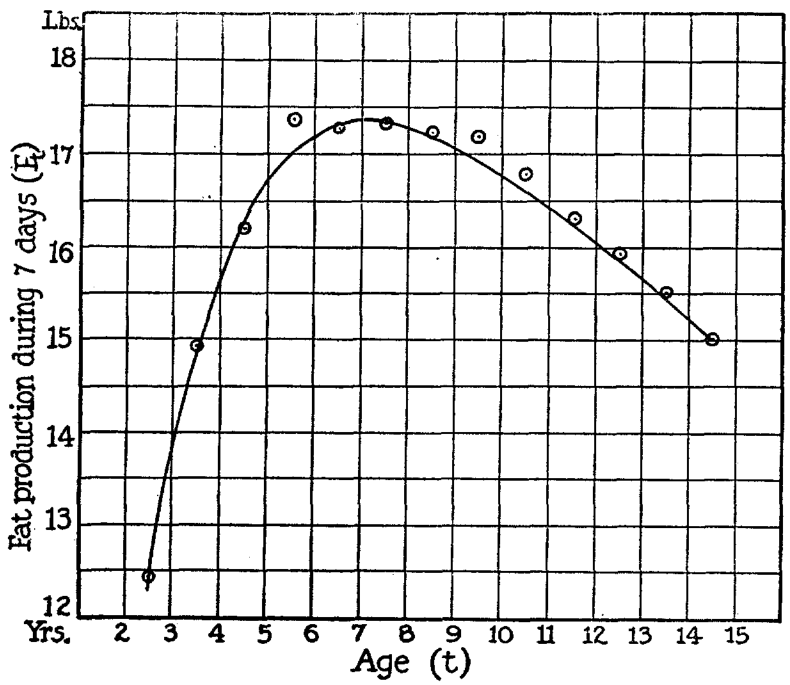

FIG. 3. Comparison between computed and observed values of milk secretion with age for 7 day records given in Table I. The circles represent observed values, the smooth line represents the equation $F = 22.1(e^{-0.026t} - 1.2e^{-0.46t})$. The observed values in this figure are based on a total of 104,560 records. The rate of senescence, it may be noted, is less steep than the rate of growth. The relative slopes of the two sides of the curve at any ages t and t_2, may be found by substituting the ages for t in the equation $\frac{dF}{dt} = 22.1(-0.026e^{-0.026t} + 1.2 \times 0.46e^{-0.46t})$.

TABLE I.

*Data on the Course of Milk Secretion with Age in the Dairy Cow.**

Age.	Ayrshire cows.		Guernsey cows.		Holstein cows. 365 day records.		Holstein cows. 305 day records.		Jersey cows.		Milking Shorthorn cows.		Weighted average of all cows.		7 day records, Holstein cows.		7 month records of a group of longlived cows.	
	No. of cows included.	Fat per yr.	No. of cows included.	Fat per yr.	No. of cows included.	Fat 365 days.	No. of cows included.	Fat 305 days.	No. of cows included.	Fat 365 days.	No. of cows included.	Fat per yr.	No. of cows included.	Fat expressed as per cent of maximum production.	No. of cows included.	Fat 7 days.	No. of cows included.	Fat per 7 mos.
yrs.		*lbs.*		*lbs.*		*lbs.*		*lbs.*		*lbs.*		*lbs.*		*per cent*		*lbs.*		*lbs.*
1.7			313	368					947	353	15	252	1,275	64.6				
2.5	1,710	350	5,241	412	2,454	508	1,200	413	4,090	383	306	272	15,001	73.6	33,765	12.46	21	24.0
3.5	903	378	2,566	452	1,523	570	762	475	2,263	443	167	285	8,184	84.0	22,019	14.91	24	28.1
4.5	716	418	1,977	492	1,238	615	606	493	1,687	486	125	352	6,349	90.4	16,374	16.20	33	33.1
5.5	545	448	1,133	511	1,116	644	467	513	1,487	502	75	376	4,823	95.5	11,259	17.39	33	35.0
6.5	399	455	897	521	835	666	331	544	1,067	516	80	383	3,609	99.1	8,356	17.26	37	37.4
7.5	298	478	572	528	583	665	223	547	837	521	66	405	2,579	100.0	5,586	17.32	32	37.1
8.5	225	453	369	527	396	659	156	566	565	524	65	402	1,776	99.1	3,256	17.25	40	38.7
9.5	155	454	264	524	232	654	72	541	355	510	43	403	1,121	97.0	1,862	17.19	39	36.9
10.5	100	472	123	512	111	652	46	529	200	509	29	411	609	95.8	1,054	16.80	39	37.9
11.5	52	423	76	486	59	650	17	538	108	513	21	369	333	92.4	548	16.34	39	33.8
12.5	26	450	32	500	37	595	13	441	58	453	13	397	179	88.3	285	15.96	32	32.1
13.5	15	436	24	447	11	569	6	510	31	470	4	399	91	85.5	130	15.54	18	33.3
14.5	8	375	5	491	4	550			13	447	3	360	33	80.2	42	15.04	15	34.8
15.5	4	392	4	446	4	475			8	451	2	353	22	79.1	24	15.40		
Total†	5,156		13,596		8,603		3,899		13,716		1,014		45,984		104,560			

* Compiled from the records of Register of Merit Jersey, Record of Merit Shorthorn, Advanced Register Ayrshire, Guernsey, and Holstein cattle.

† Total number of cows included in this table is 150,544 (exclusive of longlived cows).

this animal. The natural duration of life of the cow is said to be about 30 years. Milk records above 15 years are, however, very scarce because in addition to the accidental deaths which leave relatively few animals by the time this age is reached, the animals are also purposely disposed of due to the fact that they become increasingly unprofitable milk producers with increasing age caused by such factors as the increasing difficulty of breeding with age and decaying teeth.

While these curves represent only about half of the whole life curve, they are nevertheless of value because they show the trend of relative rates of growth and of senescence, and the age of the statistical equilibrium between these two processes. Besides, if the growth and senescence curves continue an unchanged course beyond the range of observation, as is probable, then it should be possible to extrapolate the curves by the use of some suitable formula, thereby completing the whole picture.

The trend of the curves of growth and of senescence having been determined on the basis of an extensive amount of data (there is no doubt that the data presented here are by far the largest amount that was ever brought together on the quantitative variation of milk secretion with age, and with the exception of vital statistics on man, they are the largest body of quantitative data on the change of any physiological activity with age), the next step is to formulate a mathematical expression which would not only represent the empirical curve, but what is far more important, an expression which should be rational in the sense that it is derived theoretically as a conclusion from a general law of nature, and which should be capable of explaining the mechanism of the process under investigation. Pearl and his coworkers[2] found that the expression

$$y = a + cx^2 + d \log x$$

in which y is the milk production and x is the age, may be accurately fitted to the variation of milk secretion with age. However, since

[2] Pearl, R., and Patterson, S. W., *Maine Agric. Exp. Station, Bull. 262*, 1917. Pearl, R., and Miner, J. R., *J. Agric. Research*, 1919, xvii, 285. Pearl, R., Gowen, J. W., and Miner, J. R., *Ann. Rep. Maine Agric. Exp. Station 1919*, 1919, 89. Gowen, J. W., *Genetics*, 1920, v, 111. Gowen, J. W., *Ann. Rep. Maine Agric. Exp. Station 1920*, 1920, 185.

Pearl and his coworkers do not state that this equation explains the mechanism of this variation of the activity of the mammary gland with age, or that the equation was derived as a conclusion from a general law then this is probably an empirical equation and it does not solve the problem of formulating a rational equation explaining the mechanism of the peculiar course of growth and of senescence.

The following theory is suggested as a basis for formulating a rational equation to represent the rising and falling curve of physiological activities with age and therefore as a basis for a quantitative theory of growth and senescence. It is assumed that growth and senescence go on simultaneously from the beginning to the end of life, but that the ratio between the velocities of these two processes varies in a continuous manner throughout life. At the beginning of life the ratio of growth to senescence is infinitely great, while at the time of natural death, at the extreme old age, the ratio of senescence to growth is infinitely great. At the age of maximum, or prime physical development the two processes just balance each other. The view is also adopted that growth and senescence are physicochemical processes governed by the laws of mass action—a view due to Loeb and his coworkers.[3] If growth and senescence are physicochemical processes, then the course of each, growth and senescence, should follow the course of some chemical reaction, since it is a general principle of chemistry that in a system of chemical reactions which are interdependent, the slowest reaction determines the rate of the resultant process,[4] and therefore growth and senescence while complicated processes should theoretically follow the course of chemical reactions of a simple order; and if growth and senescence go on simultaneously, but with a continuously changing ratio of velocities, then it should be possible to express the course of the whole curve of growth and senescence by the mathematical expression which represents the course of simultaneous consecutive chemical reactions. According to this theory, life may be represented symbolically by the expression $X \rightarrow Y \rightarrow Z$ in which $X \rightarrow Y$ is the process of

[3] *Cf.* (*inter alia*) Loeb, J., *Biochem. Z.*, 1906, i, 183. Loeb, J., and Lewis, W. H., *Am. J. Physiol.*, 1901–02, vi, 305. Loeb, J., and Northrop, J. H., *Proc. Nat. Acad. Sc.*, 1916, ii, 456; 1917, iii, 382. Loeb, J., *Scient. Monthly*, 1919, ix, 578.

[4] *Cf.* Walker, J., *Proc. Roy. Soc. Edinburgh*, 1897–98, xxii, 22.

growth which follows the course of a chemical reaction, or reactions, as we have indeed found in studying the growth of the dairy cow,[5] the animal under consideration, and as was found to be the case for the growth of many other organisms;[6] Y→ Z, the process of senescence which it is assumed also follows the course of, and is limited by some chemical reaction. The whole process X→ Z can therefore probably be represented by the equation of some consecutive reactions; for example,

$$M_t = A\left(ae^{-k_1 t} - be^{-k_2 t}\right) \tag{1}$$

in which k_1 and k_2 are the velocity constants respectively of senescence and growth, M_t, the milk production (or other index of physiological activity with age) at the age, t, and e, the base of natural logarithms.[7]

This equation (1) was in fact found to represent the course of milk secretion with age quite satisfactorily as may be seen in Figs. 2 and 3 where the observed values are fairly close to the values computed from this equation. This equation cannot be rigidly tested, first, because the theory of consecutive reactions is incomplete; second, because since growth and senescence are simultaneous, it is not possible to determine separately the values of the velocity constants k_1 and k_2. The satisfactory fit of the trial equation to the data is, however, extremely suggestive. The oxidation of phosphorous acid by potassium persulfate in the presence of hydriodic acid, is a classical example of consecutive simultaneous reactions. The numerical values of the velocity constants for this reaction were determined separately for the constituent reactions, the reduction of the persulfate by hydriodic acid, and the oxidation of phosphorous acid by iodine. The comparison between the theoretical and observed

[5] Brody, S., and Ragsdale, A. C., *J. Gen. Physiol.*, 1920–21, iii, 623. Brody, S., Ragsdale, A. C., and Turner, C. W., *J. Gen. Physiol.*, 1923–24, v, 445.

[6] *Cf.* (*inter alia*) Robertson, T. B., Principles of biochemistry, for students of medicine, agriculture, and related sciences, Philadelphia and New York, 1920.

[7] For derivation and application of this equation to certain life processes in plants *cf.* Osterhout, W. J. V., Injury, recovery, and death, in relation to conductivity and permeability, Monograph on Experimental Biology, Philadelphia and London, 1922.

values of this reaction *in vitro*[8] and the values obtained from trial equations and observed values in Fig. 2 and especially in Fig. 3 in the variation of milk secretion with age is not unfavorable to the latter.

The fit of the computed to the observed values of milk secretion in Fig. 1 is especially satisfactory considering some of the defects of the observed data. The most serious defect is that the population rapidly decreases with age due to the natural and purposeful elimination of the less fit animals, either because of defective physical vigor causing death at an early age, or because of unsatisfactory milk production. As a result of this elimination, and the elimination due to the minimum entrance requirements for Advanced Registry, only the better animals survive at the more advanced ages, amounting to a comparison between relatively good animals at the more advanced ages with relatively mediocre animals at the earlier ages. This would tend to a relatively higher production at the more advanced ages which may explain the fact shown in Fig. 2 that at later ages the observed production is above the computed production. The increasing difficulty of breeding animals with increasing age resulting in a longer farrow period may likewise increase the relative milk production at the later ages, since it has been shown[9] that pregnancy appreciably decreases milk production. The 7 day data shown in Fig. 3 are superior to the yearly data of Fig. 2, first, because the effect of delayed breeding due to age is absent since the 7 day records are always made before breeding; second, because the 7 day records are made when the animals are at their best, shortly after calving; and third, and most important, since the period of test is only 7 days the animals can be kept for this brief period under the very best conditions, eliminating the many unfavorable factors which come up during the course of a whole year. These uniform and favorable conditions under which the 7 day records are made therefore represent more nearly the genetic capacity of the animals than the yearly records in which environmental factors are less under control. These

[8] Federlin, W., *Z. physikal. Chem.*, 1902, xli, 565. Lewis, W. C. McC., A system of physical chemistry, London and New York, 1920, 3rd edition, 403, 4.

[9] Brody, S., Ragsdale, A. C., and Turner, C. W., *J. Gen. Physiol.*, 1922–23, v, 777.

facts and the fact that the 7 day averages are based on a very much larger number of animals than the yearly averages, may explain the better agreement between observed and computed values for the 7 day records in Fig. 3 than the yearly records in Fig. 2.

SUMMARY.

Data are presented on the effect of age on milk secretion in the dairy cow. From the age when milk secretion usually begins (2 years) to the age when maximum body weight is reached (about 8 years) increase of milk secretion and increase of body weight with age follow the same exponential course, which is the course of a monomolecular reaction of chemistry. After this age, unlike body weight which remains practically constant, milk secretion declines exponentially, that is, the course of decline follows the course of decline of a monomolecular reaction. The whole course of milk secretion with age was therefore found to follow approximately the course of two simultaneous, consecutive, monomolecular reactions. This is taken to mean that growth and senescence go on simultaneously from the beginning to the end of life, and that each follows an exponential law with age; and therefore perhaps that the course of the two processes are limited by two consecutive chemical reactions.