Comparative Growth Rates in Wild Types and Carotenoid Mutants of *Sporobolomyces salmonicolor*

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INTRODUCTION

SPOROBOLOMYCES SALMONICOLOR IS A PINK BASIDIOMYCETOUS FUNUS. WHEN A CELL PRODUCES A BUD, THE BUD IS DEVOID OF A NUCLEUS UNTIL IT IS NEARLY GROWN. AT THIS TIME, THE NUCLEUS OF THE PARENT CELL DIVIDES, ONE OF THE DAUGHTER NUCLEI PASSING INTO THE BUD AND THE OTHER REMAINING IN THE PARENT. CELLS ARE ALSO CAPABLE OF PRODUCING AERIAL STERIGMATA ON WHICH SPORES DEVELOP AND BECOME SITUATED ASYMMETRICALLY ON THE END OF THE STERIGMATA LIKE THE BASIDIOSPORES OF THE HYMENOMYCETES. JUST BEFORE THE SPORE ATTAINS FULL SIZE, A NUCLEUS MIGRATES FROM THE PARENT CELL THROUGH THE STERIGMA INTO THE SPORE. VIOLENT DISCHARGE OF THE SPORE TAKES PLACE IMMEDIATELY AFTER A DROP OF LIQUID, APPEARING AT THE HILUM OF THE SPORE, REACHES THE SIZE OF THE SPORE, BOTH SPORE AND DROP BEING SHOT AWAY TOGETHER. IT IS THEREFORE EASY TO DEVELOP COLONIES FROM SINGLE SPORES FOR GENETIC STUDY BY ISOLATION OF THE INDIVIDUAL SPORES. THE PRODUCTION OF A SINGLE STERIGMA IS APPARENTLY THE RULE FOR HEALTHY CELLS ON FRESH CULTURE MEDIUM; HOWEVER, ON AN EXHAUSTED MEDIUM, CELLS OFTEN DEVELOP TWO OR MORE

STERIGMATA. IN ADDITION, A SPORE, IF IT SHOULD FALL UPON AN EXHAUSTED MEDIUM, MAY PRODUCE ANOTHER SPORE BY REPETITION.

THE COLOR OF A PARTICULAR ISOLATE WILL BE DETERMINED BY THE NUMBER AND THE CONCENTRATION OF THE PARTICULAR PIGMENTS PRESENT. THE TYPICAL PINK WILD TYPES HAVE FIVE PIGMENTS; TORULARHODIN, GAMMA-CAROTENE, LYCOPENE, TORULIN, AND AN UNIDENTIFIED ACIDIC PIGMENT. THESE FIVE ARE PRESENT IN THE THREE WILD TYPES THAT WERE USED IN THIS INVESTIGATION. THE ORANGE MUTANT, HOWEVER, LACKS LYCOPENE AND HAS A LOW CONCENTRATION OF TORULARHODIN. THE ALBINO MUTANT DOES NOT HAVE DETECTABLE AMOUNTS OF CAROTENOID PIGMENTS AND HENCE APPEARS WHITE. OCCASIONALLY IT IS CREAM-COLORED, PROBABLY THE RESULT OF THE ACCUMULATION OF FATTY RESERVE PRODUCTS.

THE THREE WILD TYPES OCCASIONALLY PRODUCE SPONTANEOUS COLOR MUTANTS UNDER NORMAL LABORATORY CULTIVATION AND PRESUMABLY ALSO UNDER FIELD CONDITIONS. PRIOR TO THESE STUDIES AN EXTENSIVE SERIES OF PIGMENT MUTATIONS HAD BEEN INDUCED EXPERIMENTALLY

IN THE TYPE CULTURE OF Sporobolomyces salmonicolor BY TREATMENT WITH MUTAGENIC SUBSTANCES. THE TWO STRAINS USED HERE, THE ORANGE AND THE WHITE MUTANTS, WERE PRODUCED BY THE FOLLOWING SCREENING PROCEDURE.

TWENTY-FOUR HOUR CELLS OF THE TYPE CULTURE GROWN ON CUTTER'S MINIMAL AGAR WERE SUSPENDED IN A TWO PER CENT AQUEOUS SOLUTION OF URANIUM NITRATE FOR TWELVE HOURS. THE CENTRIFUGED CELLS WERE THEN WASHED IN DISTILLED WATER AND PLATED ON MINIMAL AGAR. AFTER 72 HOURS GROWTH, ANY COLONIES WHICH VARIED IN COLOR FROM THE PARENTAL CULTURE WERE SELECTED AND TRANSFERRED TO FRESH CULTURE MEDIUM. THE ALBINO STRAIN (13/13-2-50) WAS ONE OF A LARGE SERIES OF WHITE UNPIGMENTED MUTANTS THUS SELECTED .

IN A SUBSEQUENT EXPERIMENT, CELLS OF THE ALBINO STRAIN WERE TREATED IN THE SAME MANNER EXCEPT THAT THEY WERE SUSPENDED IN AN AQUEOUS SOLUTION OF COBALT NITRATE FOR TWENTY-FOUR HOURS. AMONG THE VARIANT COLONIES SELECTED WAS THE BRIGHT ORANGE STRAIN (98/98) USED IN THESE STUDIES. THIS APPARENTLY REPRESENTS A BACK MUTATION AT THE LOCI CONTROLLING

PIGMENT FORMATION. PRELIMINARY INVESTIGATION OF THESE MUTANTS IN SCREENING EXPERIMENTS WITH THE PARENTAL STRAIN INDICATED THAT BOTH THE WHITE AND THE ORANGE MUTANTS PROBABLY INVOLVED SINGLE MUTATIONS IN THE BIOSYNTHETIC PATHWAYS LEADING TO CAROTENOID SYNTHESIS. SINCE THE ISOLATION OF THESE MUTANTS IN 1948, THEY HAVE BEEN MAINTAINED IN CULTURE AND HAVE SHOWN NO TENDENCY TO REVERT TO THE PARENTAL TYPE.

THIS INVESTIGATION WAS UNDERTAKEN TO STUDY THE PHYSIOLOGY OF THE COLOR MUTANTS AND TO DETECT POSSIBLE DIFFERENCES IN METABOLIC BEHAVIOR BETWEEN THE PARENTAL STRAIN AND THE MUTANTS USING TWO ADDITIONAL WILD TYPES FOR COMPARISON.

MATERIALS AND METHODS

THE CULTURE OF SPOROBOLOMYCES SALMONICOLOR USED IN THIS INVESTIGATION WAS OBTAINED FROM C. B. VAN NIEL IN 1948 AND IS THE TYPE CULTURE FOR THE GENUS, SPOROBOLOMYCES. IT IS DESIGNATED AS 13/13 IN THIS STUDY AND IS A PINK WILD TYPE. BY TREATMENT WITH TWO PER

CENT URANIUM NITRATE, AN ALBINO MUTANT, 13/13-2-50, WAS PRODUCED FROM THE TYPE CULTURE. ANOTHER MUTANT, ORANGE IN COLOR AND DESIGNATED AS 98/98, WAS THE RESULT OF TREATING THE ALBINO MUTANT WITH TWO PER CENT COBALT NITRATE. ANOTHER WILD TYPE, USED IN THIS INVESTIGATION AND DESIGNATED AS 67/67, WHICH WAS SELECTED BY CUTTER, IS ALSO PINK. IN ADDITION, THE SEXUALLY REPRODUCING SPECIES SPORIDIOBOLUS JOHNSONII, DESIGNATED AS 166 AND OBTAINED FROM G. NYLAND IN1948, WAS INCLUDED FOR COMPARISON. IT SHOULD BE NOTED THAT ALTHOUGH THE THREE WILD TYPES ARE PINK, THERE IS A VARIANCE IN THE SHADE; 13/13 AND 67/67 ARE PALE DUSTY PINKS WHILE 166 IS A DEEP ORANGE-PINK.

DURING THIS STUDY THE BASIC MEDIUM USED WAS CUTTER'S MINIMAL AGAR, THE COMPOSITION OF WHICH IS AS FOLLOWS: NH_4NO_3, 2 GM.; KH_2PO_4, 0.5 GM.; $MgSO_4$, 0.25 GM.; DEXTROSE, 20 GM.; AGAR, 15 GM.; AND DISTILLED WATER, 1000 ML. THE pH OF THIS MEDIUM IS 4.7 ATER AUTOCLAVING AND NO FURTHER ADJUSTMENT WAS MADE. IN ADDITION, THE ORGANISMS WERE GROWN ON A COMPLETE ORGANIC MEDIUM FOR A REJUVENATING PERIOD OF THREE WEEKS, THE COMPOSI-

TION OF WHICH IS AS FOLLOWS: CANNED BEER (BUDWEISER), 8 OZ.; AGAR, 15 GM.; AND DISTILLED WATER TO 1000 ML. AFTER AUTOCLAVING THE pH IS 4.1 AND NO FURTHER ADJUSTMENT WAS MADE.

GROWTH WAS MEASURED ON 10 ML. LIQUID MINIMAL MEDIUM IN 50 ML. RYAN FLASKS. THESE WERE INOCULATED WITH 0.1 ML. OF A TWENTY-FOUR HOUR STARTER CULTURE. THE LIQUID MEDIUM IS OF THE SAME COMPOSITION STATED ABOVE BUT LACKS AGAR. ADEQUATE AMOUNTS OF OXYGEN WERE ASSURED BY SHAKING THE FLASKS 110 STROKES PER MINUTE ON AN EBERBACH RECIPROCATING SHAKER. RYAN FLASKS, MADE FROM A 50 ML. ERLENMEYER FLASK WITH A 10 ML. TEST TUBE GRAFTED ONTO ITS SIDE, WERE OBTAINED FROM MACCALASTER-BICKNELL COMPANY, NEW HAVEN, CONNECTICUT, AND BY USING THIS TYPE OF FLASK, CONTAMINATION WAS AVOIDED WHEN READINGS WERE EXTENDED OVER A PERIOD OF DAYS. A BAUSCH AND LOMB MONOCHROMATIC COLORIMETER WAS EMPLOYED TO MEASURE PER CENT OF LIGHT TRANSMITTED AT 505mμ; MO SIGNIFICANT DIFFERENCES BETWEEN READINGS WITH FILTERS OF 430, 505, 550, AND 630 mμ HAD BEEN DETECTED IN A TRIAL EXPERIMENT. AS THE CELLS GROW, THE AMOUNT OF

LIGHT TRANSMITTED DECREASES AN THE CURVE THUS OBTAINED IS THE OPPOSITE OF THE ONE USED IN TEXTBOOKS AND BASED ON DENSITY OF THE MEDIUM FOR MEASUREMENT OF GROWTH.

TO DETECT THE INFLUENCE OF ONE PURE CULTURE UPON ANOTHER, GROWING TOGETHER IN A MIXTURE, 0.1 ML. OF A ONE-TO-ONE MIXTURE OF CELLS WAS PIPETTED ONTO A PLATE OF MINIMAL AGAR AND ALLOWED TO GROW EN MASSE; OTHER PLATES WERE MADE BY STREAKING WITH 0.05 ML. OF THE CELL MIXTURE. THESE PLATES WERE INOCULATED TWO WEEKS AFTER THE FLASKS OF MIXTURES HAD BEEN INOCULATED.

STOCK CULTURES WERE MAINTAINED AT 22°C. UNDER CONSTANT FLUORESCENT LIGHT OF 350 CANDLE POWER ON 10 ML. SLANTS OF AGAR. THE LIQUID CULTURES WERE GROWN AND, GROWTH RATES MEASURED, UNDER THE SAME CONDITIONS. WHEN THE CULTURES WERE GROWN IN THE DARK, ALL LIGHT WAS EXCLUDED EXCEPT THAT ON THE SCALE OF THE COLORIMETER.

IN PLOTTING THE GROWTH CURVES ON SEMI-LOGARITHMIC PAPER, THE SCALE OF THE VERTICAL AXIS IS MODIFIED TO READ 0-20 INSTEAD OF 10-20.

OBSERVATIONS

PURE CULTURES OF THE FIVE STRAINS WERE GROWN IN THE LIGHT AND THE DARK AT 22°C. THERE WERE NO DIFFERENCES IN THE GROWTH RATES IN THE LIGHT. WHEN GROWN IN THE DARK, THE ORANGE MUTANT, 98/98, LAGGED 48 HOURS BEHIND THE OTHER STRAINS AND BECAME PIGMENTED (FIG. 1). THE OTHER STRAINS DEVELOPED PIGMENT IN THE LIGHT BUT NOT AT ALL IN THE DARK. IT WAS ALSO OBSERVED THAT THE LONGER 98/98 WAS KEPT IN THE DARK, THE LONGER ITS LAG PHASE BECAME WHEN THE ORGANISM WAS TRANSFERRED TO FRESH CULTURE MEDIUM.

WHEN THE GROWTH CURVES OF CULTURES GROWN IN THE DARK BEFORE AND AFTER TREATMENT ON BEER AGAR WERE COMPARED, AN INCREASE IN OVERALL GROWTH AND A SHORTENED LAG PHASE WAS APPARENT IN THE WILD TYPES, THAT IS, IN 166, 67/67 (FIG. 2), AND 13/13. IN THE TWO MUTANTS, HOWEVER, THE LAG PHASE WAS LENGTHENED AND GROWTH WAS NOT AS GREAT AS IT WAS BEFORE REJUVENATION (FIG. 3). IF THE FIVE CURVES ARE OVERLAID, THE LAG PHASE INCREASES PROGRESSIVELY IN THE ORDER 166, 67/67, 13/13, 13/13-2-50, 98/98. THIS PHENOMENON IS PRESENT IN BOTH SETS OF CURVES, BEFORE AND AFTER REJUVENATION (FIG. 7).

Because of the differences in the dark-grown cultures, mixtures of the pure strains were made in all possible combinations in the dark, using 0.05 ml. inoculum of each strain to give a total inoculum the same as that previously used and measured. Mixed cultures containing 166 have the same growth curve (#1), regardless of the other strain involved. This curve resembles that of pure 166 grown in the dark (Fig. 4). Cultures containing 67/67 in the mixture have the characteristic growth curve (#2), except in the presence of 166 when the curve resembles that of #1. The curve of pure 67/67 is the same as those of the mixtures, i. e., #2 (Fig, 5). Cultures containing 13/13 in the mixture have the same curve (#3), except if 166 or 67/67 is present and then the curve resembles that of the respective dominant strain (Fig. 6). Mixed cultures of the two mutants show a different growth curve (#4) from those exhibited when the wild type strains are present.

The lag phase is lengthened progressively proceeding from #1 to #4, as was true in the pure cultures both before and after treatment with beer (Fig. 8). In the case

OF THE TWO MUTANTS, HOWEVER, THE LAG PHASE IS SHORTENED IN THE PRESENCE OF THE PARENTAL CULTURE, 13/13, YET THIS STRAIN IS NOT STRONG ENOUGH TO INFLUENCE THE GROWTH RATE OF EITHER MUTANT TO THE POINT THAT THE CURVE OF 13/13 IN PURE CULTURE IS ATTAINED. THE ALBINO MUTANT, 13/13-2-50, SHORTENS THE LAG PHASE OF THE MIXTURE WHEN IT IS COMBINED WITH 98/98, BUT ALSO IS NOT STRONG ENOUGH TO ATTAIN ITS OWN CURVE IN PURE CULTURE.

WHEN THE PLATES INOCULATED FROM THE MIXTURES WERE EXAMINED, THEY WERE COMPARED WITH PLATES MADE FROM THE STOCK CULTURES IN WHICH THE PURE CULTURES WERE STREAKED ACROSS ONE ANOTHER SO THAT A MIXTURE OF THE TWO COULD BE OBSERVED IN THE MIDDLE. THE COLOR OF THE MIXTURES WAS MODIFIED FROM THAT OF THE PURE CULTURES EXCEPT IN THE FOLLOWING CASES: 98/98 AND 166; 98/98 AND 67/67; AND 67/67 AND 13/13-2-50, WHERE NO WHITE COLONIES COULD BE SEEN. IN 98/98 AND 13/13-2-50 THERE WERE APPROXIMATELY TEN WHITE COLONIES TO ONE ORANGE COLONY. IN ADDITION, THE THEORETICAL AVERAGE GROWTH RATES OF THE TWO PURE CULTURES WERE COMPARED WITH THE AVERAGE GROWTH RATES OF THE ACTUAL MIXED CULTURES. A RANGE OF 2.5 UNITS ON

EITHER SIDE OF THE AVERAGE FIGURES SHOULD BE SUFFICIENT TO ACCOUNT FOR EXPERIMENTAL ERRORS (TABLE I).

DISCUSSION

BEADLE AND TATUM PROPOSED THE HYPOTHESIS THAT ONE GENE CONTROLS ONE ENZYME AND BY THE BLOCKAGE OF A PARTICULAR GENE, ONLY ONE BIOCHEMICAL PATHWAY IS AFFECTED. IN THIS STUDY, MUTANTS, SELECTED FOR THEIR COLOR VARIATION FROM THE PARENTAL STRAIN, DISPLAYED A GROWTH DIFFERENCE FROM THE PARENTAL STRAIN WHEN CULTURED IN THE DARK. THE MUTANTS ARE CONSIDERED TO INVOLVE ONLY ONE-GENE CHANGES AND THEREFORE THE DATA PRESENTED HERE APPEARS TO CONTRADICT THEIR HYPOTHESIS. THE ENZYME PRESUMABLY BLOCKED MAY BE INVOLVED IN ANOTHER BIOCHEMICAL PATHWAY IN ADDITION TO THAT OF CAROTENOID SYNTHESIS. THERE IS ALSO THE POSSIBILITY THAT THE CAROTENOID COMPOUND BLOCKED IS NECESSARY FOR GROWTH; THE CAROTENOID PIGMENTS CAN SERVE AS AUXILLARY ENERGY TRAPS IN A MANNER SIMILAR TO THE MECHANISM OF CHLOROPHYLL.

THE DIFFERENT STRAINS HAVE THE ABILITY TO INFLUENCE

ONE ANOTHER'S GROWTH IF GROWN TOGETHER. AFTER 48 HOURS, ONE OF THE TEN COMBINATIONS DISPLAYED LESS GROWTH THAN WAS EXPECTED FROM THE AVERAGE OF THE PURE CULTURES; THIS WAS THE MIXTURE OF THE ALBINO AND ORANGE MUTANTS, BOTH OF WHICH, WHEN GROWN PURE IN THE DARK, SHOWED LESS GROWTH AND SLOWER GROWTH RATES THAN THE PARENTAL STRAIN. THREE OF THE TEN COMBINATIONS CONTAINED A WILD TYPE AND A MUTANT; THESE DISPLAYED GREATER GROWTH AT THIS TIME. IN TWO OF THE THREE THERE IS NO MODIFICATION OF COLOR WHEN PLATED ON AGAR. THERE APPEARS TO BE SOME GROWTH-ENHANCING MATERIAL PROVIDED BY THE WILD TYPE STRAIN WHICH THE ORANGE MUTANT REQUIRES IN ORDER TO GROW AT THE SAME RATE AS THE PARENT STRAIN OR WILD TYPE.

HOWEVER, AFTER 108 HOURS, ALL BUT TWO OF THE COMBINATIONS DISPLAY GREATER GROWTH THAN EXPECTED. IN THE MIXTURE OF THE ALBINO MUTANT AND A WILD TYPE, WHEN EXAMINED ON AGAR PLATES, NO WHITE COLONIES WERE DETECTABLE AND THE COLOR OF THE MIXTURE WAS NOT MODIFIED FROM THAT OF THE PARENT STOCK CULTURES. THE STRONGER OR MORE DOMINANT STRAINS WERE ABLE TO INDUCE GREATER GROWTH ON THE PART OF THEIR GROWING PARTNER IN THE MIXTURE. FROM THE

COLOR MODIFICATIONS IN MIXTURES, ONE MIGHT BE LED TO BELIEVE THAT THERE WAS EITHER A TRANSFER OF GENETIC MATERIAL OR AN INHIBITION OF COLOR-PRODUCING ABILITY IN THE WILD TYPES BROUGHT ABOUT BY GROWTH IN CLOSE PROXIMITY TO THE MUTANTS. THE AVAILABLE DATA DOES NOT ALLOW VALID SPECULATION ON THESE TWO ALTERNATIVE EXPLANATIONS.

IN THE LITERATURE, HOWEVER, DATA HAS BEEN PRESENTED TO UPHOLD THE HYPOTHESIS THAT ONE GENE CONTROLS THE ACTIVITY OF ONE ENZYME. SRB AND HOROWITZ INVESTIGATED 15 STRAINS OF NEUROSPORA, EACH OF WHICH REQUIRES ARGININE OR A RELATED COMPOUND FOR NORMAL GROWTH. FROM THE RESULTS IT WAS EVIDENT THAT THE ONE GENE-ONE ENZYME HYPOTHESIS APPLIES TO THIS SERIES OF REACTIONS. ON THE OTHER HAND, THE FACT THAT A SINGLE GENE SUBSTITUTION MAY MODIFY OTHER REACTIONS IS QUITE WIDELY DISCUSSED IN THE LITERATURE. THE CREEPER FOWL, STUDIED BY LANDAUER AND HIS ASSOCIATES, IS A GOOD EXAMPLE. HETEROZYGOUS BIRDS HAVE SHORTENED LONG BONES AND THE ADULT IS A DISPROPORTIONATE DWARF. THE HOMOZYGOTE WITH THE DOUBLE RECESSIVE CHARACTER DIES BEFORE HATCHING AND SHOWS

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MANY ADDITIONAL ABNORMALITIES. IN ADDITION, GRÜNBERG HAS DISCUSSED THE QUESTION OF PLEIOTROPIC GENE EFFECTS AND COMES TO THE CONCLUSION THAT PROBABLY MOST IF NOT ALL GENES PRIMARILY INFLUENCE ONE PROCESS THAT IS CELL- OR TISSUE-SPECIFIC.

THE EVIDENCE PRESENTED IN THIS PAPER INDICATES THAT THE ONE GENE-ONE ENZYME HYPOTHESIS DOES NOT HOLD TRUE FOR THIS SERIES OF REACTIONS, BUT FURTHER WORK MUST BE DONE BEFORE A DEFINITE STATEMENT CAN BE MADE.

Table I

STRAIN COMBINATION	Average per cent light transmitted	
	48 hours	
	Theoretical Pure	Actual Mixed
13/13 & 13/13-2-50	28.5	27.5
13/13 & 67/67	16.5	13.0
13/13 & 98/98	53.7	27.0
13/13 & 166	15.2	9.5
13/13-2-50 & 67/67	19.7	18.5
13/13-2-50 & 98/98	56.7	79.5
13/13-2-50 & 166	14.2	8.5
67/67 & 98/98	45.0	10.0
67/67 & 166	6.5	11.5
98/98 & 166	43.5	6.5
	108 hours	
13/13 & 13/13-2-50	21.5	12.5
13/13 & 67/67	12.3	5.0
13/13 & 98/98	34.0	13.5
13/13 & 166	11.5	4.0
13/13-2-50 & 67/67	12.8	8.0
13/13-2-50 & 98/98	44.5	7.5
13/13-2-50 & 166	12.0	4.0
67/67 & 98/98	25.3	4.5
67/67 & 166	2.8	5.5
98/98 & 166	24.5	3.0

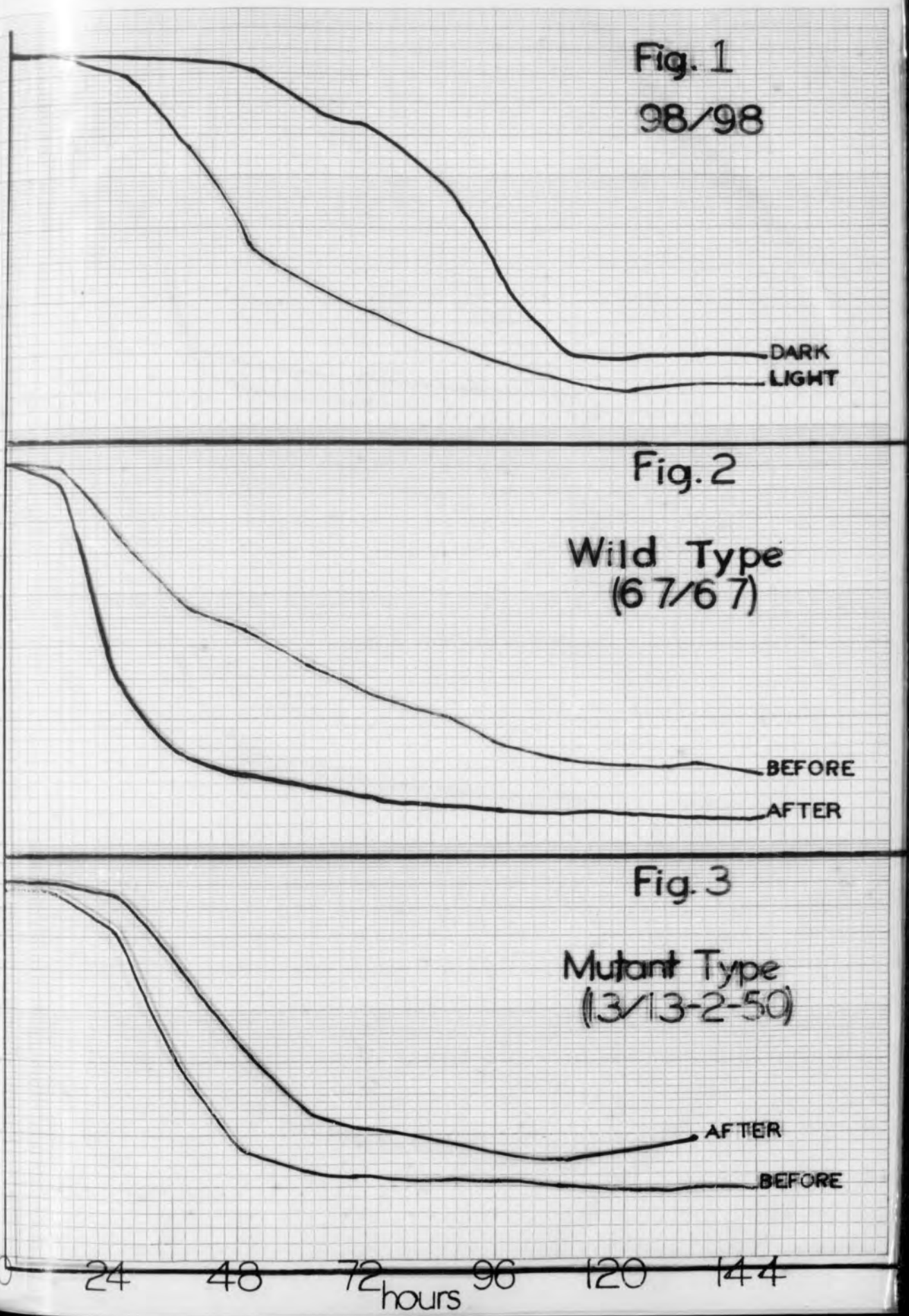
Fig. 1
98/98
DARK
LIGHT
Fig. 2
Wild Type
(67/67)
BEFORE
AFTER
Fig. 3
Mutant Type
(13/13-2-50)
AFTER
BEFORE
0
24
48
72
hours
96
120
144

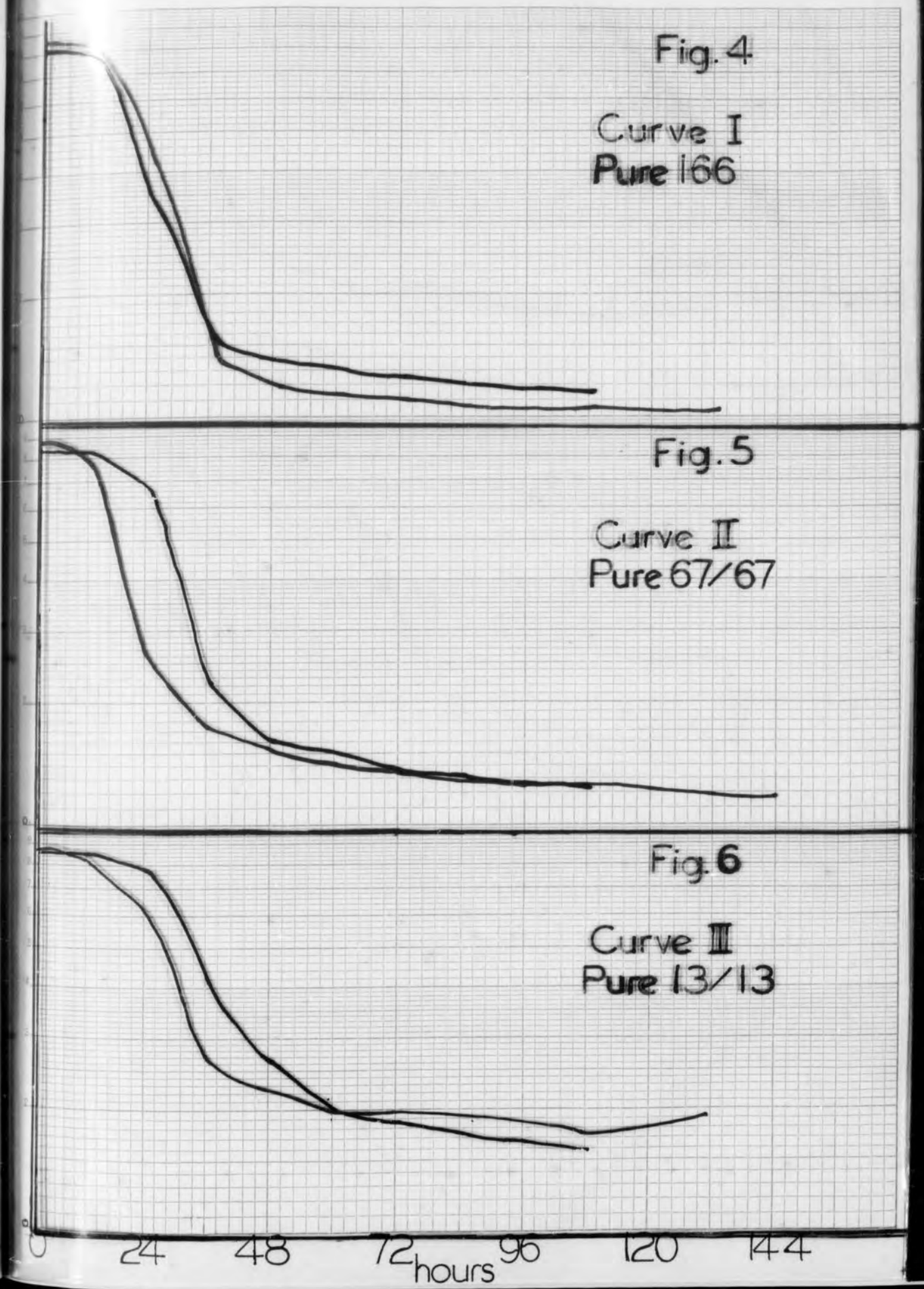
Fig. 4
Curve I
Pure 166
Fig. 5
Curve II
Pure 67/67
Fig. 6
Curve III
Pure 13/13
0
24
48
72
hours
96
120
144

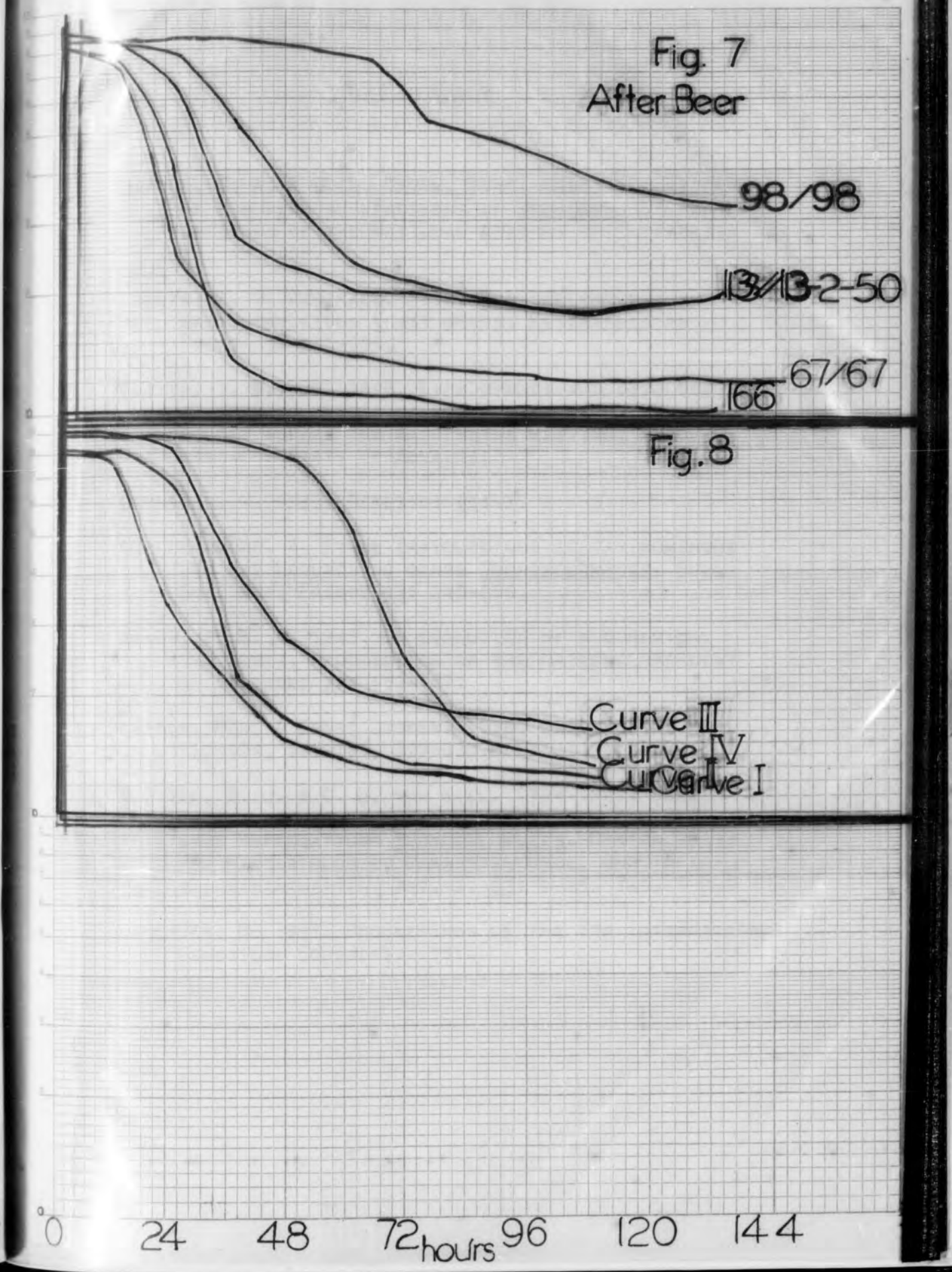
Fig. 7
After Beer
98/98
13/13-2-50
67/67
166
Fig. 8
Curve III
Curve IV
Curve I
0
24
48
72 hours
96
120
144

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