



(19) 대한민국특허청(KR)
(12) 등록특허공보(B1)

(45) 공고일자 2024년11월12일
(11) 등록번호 10-2729669
(24) 등록일자 2024년11월08일

(51) 국제특허분류(Int. Cl.)
C12N 15/113 (2010.01) C12N 15/10 (2017.01)
C12N 15/63 (2006.01) C12N 15/90 (2006.01)
C12N 9/22 (2006.01)
(52) CPC특허분류
C12N 15/1132 (2013.01)
C12N 15/102 (2013.01)
(21) 출원번호 10-2018-7012502
(22) 출원일자(국제) 2016년10월07일
심사청구일자 2021년10월06일
(85) 번역문제출일자 2018년05월02일
(65) 공개번호 10-2018-0054871
(43) 공개일자 2018년05월24일
(86) 국제출원번호 PCT/US2016/055916
(87) 국제공개번호 WO 2017/062723
국제공개일자 2017년04월13일
(30) 우선권주장
62/239,239 2015년10월08일 미국(US)
(56) 선행기술조사문헌
POLS ONE, 제10권, 4호, e0122059, 1-18
면(2015.04.24.)
WO2015031775 A1
EP01582591 A1

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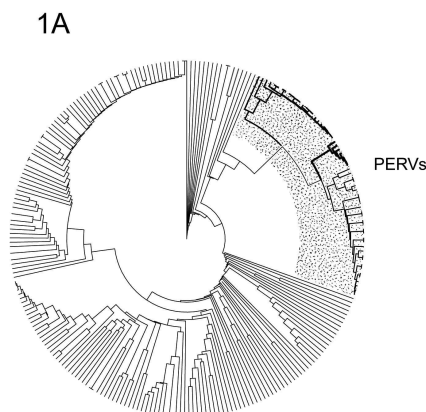
심사관 : 문동현

(54) 발명의 명칭 다중화 게놈 편집

(57) 요약

1개 이상의 표적 핵산 서열의 각각의 전부 또는 일부와 상보적인 부분을 포함하는 1개 이상의 리보핵산 (RNA) 서열, 및 Cas 단백질을 코딩하는 핵산 서열을 세포 내로 도입하고, Cas 단백질이 발현되고 Cas 단백질이 세포에서 1개 이상의 표적 핵산 서열을 결합시키고 조정하는 조건 하에서 세포를 유지하는 것을 포함하는 세포에서 유전자의 일부 또는 전부의 카피를 조정하는 방법이 제공된다.

대표도



(52) CPC특허분류

C12N 15/63 (2013.01)

C12N 15/907 (2013.01)

C12N 9/22 (2013.01)

C12N 2310/20 (2017.05)

명세서

청구범위

청구항 1

유전적으로 조작된 돼지 세포로서, 적어도 97%의 돼지 내인성 레트로바이러스 (PERV) *pol* 유전자는 유전적으로 조작된 게놈 indel을 포함하는 것인, 유전적으로 조작된 돼지 세포.

청구항 2

제1항에 있어서, 100%의 PERV *pol* 유전자가 유전적으로 조작된 게놈 indel을 포함하는 것인, 유전적으로 조작된 돼지 세포.

청구항 3

제1항 또는 제2항에 있어서, 야생형 돼지 세포와 제2 세포의 공동-배양과 비교하여 유전적으로 조작된 돼지 세포와 제2 세포의 공동-배양에 의해 입증된 바와 같이 PERV 전파의 적어도 1000배 감소를 나타내는, 유전적으로 조작된 돼지 세포.

청구항 4

제3항에 있어서, 제2 세포가 인간 세포이며, 임의로 상기 인간 세포가 HEK293인, 유전적으로 조작된 돼지 세포.

청구항 5

제1항에 있어서, 유전적으로 조작된 게놈 indel이 시퀀싱에 의해 관찰되는 것인 유전적으로 조작된 돼지 세포.

청구항 6

제1항에 있어서, 원형(intact) PERV *gag* 및/또는 *env* 유전자를 함유하는 유전적으로 조작된 돼지 세포.

청구항 7

제1항의 유전적으로 조작된 돼지 세포로부터 유래된 자손 세포.

청구항 8

복수의 제7항의 자손 세포를 포함하는 조성물.

청구항 9

복수의 유전적으로 조작된 돼지 세포를 포함하는 단리된 돼지 장기로서, 상기 복수의 유전적으로 조작된 돼지 세포 중의 각 유전적으로 조작된 돼지 세포는, 적어도 97%의 PERV *pol* 유전자가 유전적으로 조작된 게놈 indel을 포함하는 것을 특징으로 하는 것인 단리된 돼지 장기.

청구항 10

제9항에 있어서, 100%의 PERV *pol* 유전자가 유전적으로 조작된 게놈 indel을 포함하는 것인, 단리된 돼지 장기.

청구항 11

제9항 또는 제10항에 있어서, 각 유전적으로 조작된 돼지 세포가, 야생형 돼지 세포와 인간 세포의 공동-배양과 비교하여 유전적으로 조작된 돼지 세포와 인간 세포의 공동-배양에 의해 입증된 바와 같이 PERV 전파의 적어도 1000배 감소를 나타내는 것인, 단리된 돼지 장기.

청구항 12

제11항에 있어서, 인간 세포가 HEK293인, 단리된 돼지 장기.

청구항 13

제9항에 있어서, 유전적으로 조작된 게놈 indel이 시퀀싱에 의해 관찰되는 것인 단리된 돼지 장기.

청구항 14

제9항에 있어서, 유전적으로 조작된 돼지 세포가 원형 PERV *gag* 및/또는 *env* 유전자를 함유하는 것인 단리된 돼지 장기.

청구항 15

제1항에 있어서, 배아 또는 접합체로부터인 유전적으로 조작된 돼지 세포.

청구항 16

제1항에 있어서, 배선 세포인 유전적으로 조작된 돼지 세포.

청구항 17

제1항에 있어서, 줄기 세포인 유전적으로 조작된 돼지 세포.

청구항 18

제17항에 있어서, 줄기 세포가 배아 줄기 세포 또는 다능성 줄기 세포인 유전적으로 조작된 돼지 세포.

청구항 19

제1항에 있어서, 체세포인 유전적으로 조작된 돼지 세포.

청구항 20

삭제

청구항 21

삭제

청구항 22

삭제

청구항 23

삭제

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삭제

청구항 56

삭제

발명의 설명

기술 분야

[0001] 관련 출원 데이터

[0002] 본 출원은 2015년 10월 8일에 출원된 미국 가출원 번호 62/239,239에 대해 우선권 주장하며, 이는 모든 목적을 위해 그 전문이 본원에 참조로 포함된다.

배경 기술

[0003] 서열-특이적 뉴클레아제를 통한 게놈 편집이 공지되어 있다. 게놈에서의 뉴클레아제-매개된 이중-가닥 DNA(dsDNA) 파단은 2가지 주요 메커니즘에 의해 복구될 수 있다: 빈번히 비-특이적 삽입 및 결실(indel)의 도입을 초래하는 비-상동 말단 연결(NHEJ), 또는 복구 주형으로서 상동 가닥을 혼입하는 상동성 지정 복구(HDR). 그 전문이 본원에 참조로 포함되는 참고문헌 4를 참조한다. 서열-특이적 뉴클레아제가 바람직한 돌연변이를 함유

하는 상동 공여자 DNA 구축물과 함께 전달되는 경우, 유전자 표적화 효율은 단지 공여자 구축물 단독에 비해 1000배 증가된다.

[0004] 부위-특이적 뉴클레아제의 DNA 또는 mRNA를 1개의 세포 배아 내로 직접 주입하여 다양한 종에서 특정된 로커스에서 DNA 이중 가닥 파단 (DSB)을 생성함으로써 게놈 변형의 프로세스를 가속화하는 대안적 방법이 개발된 바 있다. 이들 부위-특이적 뉴클레아제에 의해 유도된 DSB는 그 후 커팅 부위에서 결실 또는 삽입을 운반하는 돌연변이체 마우스 및 래트를 초래하는 오류-유발 비-상동 말단 연결 (NHEJ)에 의해 복구될 수 있다. DSB에 플랭킹된 말단과 상동성을 갖는 공여자 플라스미드가 공동-주입되는 경우, 고-충실도 상동 재조합은 표적화된 통합을 갖는 동물을 생성할 수 있다. 이들 방법은 각각의 표적 유전자에 대한 아연 손가락 뉴클레아제 (ZNF) 또는 전사 활성화제-유사 이펙터 뉴클레아제 (TALEN)의 복잡한 설계를 요구하기 때문에, 그리고 표적화의 효율은 실질적으로 다양할 수 있기 때문에, 다중화 유전자 표적화는 지금까지 보고된 바 없다.

[0005] 따라서, 돼지와 같은 동물을 생성하기 위한 유전적으로 변형된 세포를 제조하는 개선된 방법은 이식용 장기의 잠재적 공급원을 위해 필요하다.

발명의 내용

[0006] 세포에서 다중 핵산 서열의 매우 효율적이며 동시적인 표적화를 달성하기 위한 규칙적 간격으로 군발하는 짧은 회문구조 반복서열 (Clustered Regularly Interspaced Short Palindromic Repeats) (CRISPR) 및 CRISPR 연관된 (Cas) 단백질 (CRISPR/Cas) 시스템의 용도가 본원에 기재된다.

[0007] 본 개시내용의 측면은 효소가 DNA를 커팅하고, 외인성 공여자 핵산이 예컨대 상동 재조합에 의해 DNA 내로 삽입되는, 세포에 의해 발현되는 뉴클레아제 활성을 갖는 효소, 예컨대 뉴클레아제 활성을 갖는 DNA 결합 단백질을 DNA (데옥시리보핵산) 상의 표적 위치로 지정하기 위한 1개 이상의 가이드 RNA (리보핵산)를 사용한 세포 (예를 들어, 줄기 세포, 체세포, 배선 세포, 접합체)에서의 게놈 DNA의 변형, 예컨대 DNA의 다중화 변형에 관한 것이다. 본 개시내용의 측면은 세포 내에 DNA의 다중 변형을 갖는 세포를 생성하기 위한 세포에서의 DNA 변형의 주기화 또는 반복 단계를 포함한다. 변형은 외인성 공여자 핵산의 삽입을 포함할 수 있다. 변형은 내인성 핵산의 결실을 포함할 수 있다.

[0008] 다중 핵산 서열은 효소, 및 복수의 RNA를 코딩하는 핵산을 발현하는 세포 내로, 예컨대 RNA가 발현되고, 복수에서의 각각의 RNA가 효소를 DNA의 특정 부위에 가이딩하고, 효소가 DNA를 커팅하는 공동-형질전환에 의해 도입하는 단일 단계에 의해 조정될 (예를 들어, 불활성화될) 수 있다. 이러한 측면에 따르면, 세포에서의 DNA의 많은 변경 또는 변형은 단일 주기로 생성된다.

[0009] 한 측면에 따르면, 효소를 발현하는 세포는 예컨대 효소를 코딩하고, 세포에 의해 발현될 수 있는 핵산을 세포 내로 도입함으로써 효소를 발현하도록 유전적으로 변경되었다. 이러한 방식에서, 본 개시내용의 측면은 효소를 발현하는 세포 내로 RNA를 도입하는 단계, 외인성 공여자 핵산을 세포 내로 도입하는 단계, RNA를 발현시키는 단계, RNA, 효소 및 DNA의 공동-국재화 복합체를 형성하는 단계, 및 효소에 의해 DNA를 효소적 커팅하는 단계를 주기화하는 것을 포함한다. DNA 내로의 공여자 핵산의 삽입은 또한 본원에서 제공된다. 상기 단계의 주기화 또는 반복은 다중 로커스에서의 세포의 다중화 유전적 변형, 즉, 다중 유전적 변형을 갖는 세포를 초래한다.

[0010] 특정 측면에 따르면, 본 개시내용의 범위 내의 DNA 결합 단백질 또는 효소는 가이드 RNA와, 및 복합체를 복합체가 DNA 서열에 결합하는 이중 가닥 DNA 서열에 가이딩하는 가이드 RNA와 복합체를 형성하는 단백질을 포함한다. 한 측면에 따르면, 효소는 RNA 가이딩된 DNA 결합 단백질, 예컨대 DNA에 결합하고, RNA에 의해 가이딩되는 유형 II CRISPR 시스템의 RNA 가이딩된 DNA 결합 단백질일 수 있다. 한 측면에 따르면, RNA 가이딩된 DNA 결합 단백질은 Cas9 단백질이다.

[0011] 본 개시내용의 이러한 측면은 이중 가닥 DNA에의 또는 이와는 RNA 및 DNA 결합 단백질의 공동-국재화로 지칭될 수 있다. 이러한 방식에서, DNA 결합 단백질-가이드 RNA 복합체는 다중 유전적 변형, 예컨대 유전자의 1개 이상의 (예를 들어, 모든) 카피의 파괴를 갖는 세포를 생성하도록 이중 가닥 DNA의 다중 부위를 커팅하는데 사용될 수 있다.

[0012] 특정 측면에 따르면, (a) 표적 DNA와 상보적인 1개 이상의 RNA를 코딩하고, 효소를 표적 DNA에 가이딩하는 제1 외래 핵산을 세포 내로 도입하며, 여기서 1개 이상의 RNA 및 효소는 표적 DNA에 대한 공동-국재화 복합체의 구성원이고, 1개 이상의 RNA 및 효소는 표적 DNA를 공동-국재화하고, 효소는 표적 DNA를 절단하여 세포에서 변경된 DNA를 생성하는 단계, 및 단계 (a)를 다수회 반복하여 세포에서 DNA에 대한 다중 변경을 생성하는 것을 포함

하는, 표적 DNA와 상보적인 RNA와 공동-국제화 복합체를 형성하고, 표적 DNA를 부위 특이적 방식으로 절단하는 효소를 발현하는 세포에서 표적 DNA에 대한 다중 변형을 생성하는 방법이 제공된다.

- [0013] 일부 측면에서, 세포에서 1개 이상의 표적 핵산 서열의 발현을 불활성화시키는 방법은 1개 이상의 표적 핵산 서열의 각각의 전부 또는 일부와 상보적인 부분을 포함하는 1개 이상의 리보핵산 (RNA) 서열, 및 Cas 단백질을 코딩하는 핵산 서열을 세포 내로 도입하고; Cas 단백질이 발현되고 Cas 단백질이 세포에서 1개 이상의 표적 핵산 서열에 결합하여 그를 불활성화시키는 조건 하에서 세포를 유지하는 것을 포함한다.
- [0014] 다른 측면에서, 세포에서 1개 이상의 표적 핵산 서열을 조정하는 방법은 세포에서 표적 핵산 서열의 전부 또는 일부와 상보적인 RNA를 코딩하는 핵산 서열을 세포 내로 도입하고; RNA와 상호작용하고 표적 핵산 서열을 부위 특이적 방식으로 절단하는 효소를 코딩하는 핵산 서열을 세포 내로 도입하고; RNA가 복합체를 형성하는 상보적 표적 핵산 서열에 결합하는 조건 하에서 세포를 유지하는 것을 포함하며, 여기서 효소는 복합체 상의 결합 부위에 결합하고 1개 이상의 표적 핵산 서열을 조정한다.
- [0015] 본원에 기재된 방법에서, 도입 단계는 세포를 1개 이상의 RNA 서열, 및 Cas 단백질을 코딩하는 핵산 서열로 형질감염시키는 것을 포함할 수 있다.
- [0016] 일부 실시양태에서, 1개 이상의 RNA 서열, Cas 단백질을 코딩하는 핵산 서열, 또는 이들의 조합은 세포의 계놈 내로 도입된다.
- [0017] 일부 실시양태에서, Cas 단백질의 발현이 유도된다.
- [0018] 본원에 기재된 방법에서, 세포는 배아로부터의 것이다. 세포는 줄기 세포, 접합체, 또는 배선 세포일 수 있다. 세포가 줄기세포인 실시양태에서, 줄기 세포는 배아 줄기 세포 또는 다능성 줄기 세포이다. 다른 실시양태에서, 세포는 체세포이다. 세포가 체세포인 실시양태에서, 체세포는 진핵 세포 또는 원핵 세포이다. 진핵 세포는 동물 세포, 예컨대 돼지, 마우스, 래트, 토끼, 개, 말, 소, 비-인간 영장류, 인간으로부터의 것일 수 있다.
- [0019] 1개 이상의 표적 핵산 서열은 돼지 내인성 레트로바이러스 (PERV) 유전자를 포함할 수 있다. 예를 들어, PERV 유전자는 *pol* 유전자를 포함할 수 있다.
- [0020] 본원에 기재된 방법은 *pol* 유전자의 1개 이상의 카피를 불활성화시키거나, 조정하거나, 실행할 수 있다. 일부 실시양태에서, 세포에서의 *pol* 유전자의 모든 카피는 불활성화된다.
- [0021] 일부 실시양태에서, Cas 단백질은 Cas9이다.
- [0022] 일부 실시양태에서, 1개 이상의 RNA 서열은 약 10 내지 약 1000개 뉴클레오타이드일 수 있다. 예를 들어, 1개 이상의 RNA 서열은 약 15 내지 약 200개 뉴클레오타이드일 수 있다.
- [0023] 일부 측면에서, 조작된 세포는 1개 이상의 내인성 바이러스 유전자; 및 1개 이상의 내인성 바이러스 유전자의 1개 이상의 표적 핵산 서열의 전부 또는 일부와 상보적인 부분을 포함하는 1개 이상의 외인성 핵산 서열을 포함하며; 여기서 세포의 1개 이상의 내인성 바이러스 유전자의 각각은 조정된다.
- [0024] 또 다른 측면에서, 조작된 세포는 복수의 내인성 레트로바이러스 유전자; 및 복수의 내인성 바이러스 유전자의 1개 이상의 표적 핵산 서열의 전부 또는 일부와 상보적인 부분을 포함하는 1개 이상의 외인성 핵산 서열을 포함할 수 있으며; 여기서 세포의 복수의 내인성 바이러스 유전자의 각각은 조정된다.
- [0025] 본원에 기재된 조작된 세포는 돼지 내인성 레트로바이러스 (PERV) 유전자를 포함할 수 있다. 예를 들어, PERV 유전자는 *pol* 유전자를 포함할 수 있다.
- [0026] 일부 측면에서, *pol* 유전자의 조정은 *pol* 유전자의 1개 이상의 카피를 불활성화시킨다. 예를 들어, 세포에서 *pol* 유전자의 모든 또는 실질적으로 모든 카피가 불활성화된다.
- [0027] 한 측면에 따르면, RNA는 약 10 내지 약 1000개 뉴클레오타이드이다. 한 측면에 따르면, RNA는 약 20 내지 약 100개 뉴클레오타이드이다.
- [0028] 한 측면에 따르면, 1개 이상의 RNA는 가이드 RNA이다. 한 측면에 따르면, 1개 이상의 RNA는 tracrRNA-crRNA 융합물이다.
- [0029] 한 측면에 따르면, DNA는 계놈 DNA, 미토콘드리아 DNA, 바이러스 DNA, 또는 외인성 DNA이다.

도면의 간단한 설명

[0030]

도 1A-1C는 CRISPR-Cas9 gRNA가 PK15 세포에서 PERV의 62개 카피에서 pol 유전자를 특이적으로 표적화하도록 설계되었음을 도시한다. (A) 돼지 계놈에 존재하는 내인성 레트로바이러스를 나타내는 계통수. PERV는 청색으로 강조되어 있다. (B) 디지털 액적 PCR을 통한 PK15 세포에서의 PERV의 카피 수 측정. pol 요소의 카피 수를 3가지 독립적 참조 유전자: ACTB, GAPDH, 및 EB2를 사용하여 62로 추정하였다. N=3, 평균 +/- SEM. (C) 2개의 CRISPR-Cas9 gRNA를 PERV pol 유전자의 촉매 영역을 표적화하도록 설계하였다. 2개의 gRNA 표적화 서열을 하기에 PERV 유전자 구조의 개략도로 나타낸다. 그들의 PAM 서열은 적색으로 강조되어 있다. (서열식별번호 (SEQ ID NO): 27-28)

도 2A-2B는 Cas9 처리 후의 PERV pol 유전자의 모든 카피의 불활성화를 갖는 클론 PK15 세포를 도시한다. (A) pol 표적화 효율의 이중모드 분포가 Cas9 유도의 17일 후에 단일-세포-유래된 PK15 클론 중에서 관찰되었다. 45/50은 <16% 표적화 효율을 나타내었고; 5/50 클론은 >93% 표적화 효율을 나타내었다. (B) CRISPR-Cas9 처리 후의 PERV pol 로커스에서의 PK15 반수체형. 적색에서, PERV pol 서열에서의 indel 사건을 나타낸다. 보라색의 음영은 내인성 PERV를 지시한다.

도 3A-3D는 하기를 도시한다: (A) 5일 및 7일 동안 PK15 세포와의 공동-배양 후의 HEK-293-GFP 세포의 계놈 (각각 293G5D 및 393G7D)에서의 PERV pol, gag, 및 env DNA의 검출. 돼지 GGTA1 프라이머 세트를 사용하여 정제된 인간 세포의 돼지 세포 오염을 검출하였다. (B) 특이적 프라이머 세트를 사용한 야생형 PK15 세포와 공동-배양된 집단으로부터 유래된 1000개의 293G 세포에서의 PERV 요소의 수의 qPCR 정량화. (N=3, 평균+/-SEM) (C) 높은 수준의 PERV pol 변형을 갖는 PK15 클론 15, 20, 29, 및 38, 및 최소로 변형된 클론 40 및 41에서의 PERV 요소의 수의 qPCR 정량화. (N=3, 평균+/-SEM) (D) 고도로 변형된 PK15 클론 20 및 최소로 변형된 클론 40과 함께 이전에 배양된 집단으로부터 단리된 다양한 수의 HEK 293-GFP 세포 (0.1, 1, 10, 및 100)로부터의 계놈 DNA 상의 PERV pol에 대한 PCR의 결과. PCR 반응의 전체 패널에 대해서는 도 S18-21을 참조한다.

도 4 (S1)는 PERV pol 컨센서스 서열 및 gRNA 설계를 도시한다.

도 5 (S2)는 CRISPR/Cas9 구축물 표적화 PERV의 개략도이다.

도 6 (S3)은 Cas9-gRNA 활성의 측정을 도시한다.

도 7 (S4)은 PERV 표적화를 위한 Cas9 발현을 유도하는 DOX 농도의 최적화를 도시한다.

도 8 (S5)은 PiggyBac-Cas9/gRNA PERV 표적화 효율의 시계열 측정을 도시한다.

도 9 (S6)는 렌티(Lenti)-Cas9/2gRNA PERV 표적화 효율의 시계열 측정을 도시한다.

도 10 (S7)은 PERV 표적화 효율 및 indel 패턴화의 생어(Sanger) 시퀀싱 확인을 도시한다. (서열식별번호: 29)

도 11 (S8)은 반복된 유전자 편집 실험을 도시한다.

도 12A-B (S9)는 단일 세포의 PERV pol 표적화 효율을 도시한다.

도 13 (S10)은 PERV 반수체형의 계통발생을 도시한다.

도 14 (S11)는 pol 유전자 파괴의 분포를 도시한다.

도 15A-15B (S12)는 고도로 및 저도로 변형된 PK15 클론의 핵형 분석을 도시한다.

도 16 (S13)은 PK15 클론의 핵형 분석의 요약을 도시한다.

도 17 (S14)은 핵형 명명법을 도시한다.

도 18 (S15)은 PERV 역전사효소 활성의 검출을 도시한다.

도 19 (S16)는 인간 세포에의 PERV의 전파를 검출하기 위한 실험 설계를 도시한다.

도 20A-20C (S17)는 FACS에 의한 정제된 HEK293-GFP 세포의 품질 제어를 도시한다.

도 21A-21D (S18)는 돼지 GGTA1프라이머를 사용한 HEK293 세포에서의 돼지 세포 오염의 검출을 도시한다.

도 22A-22D (S19)는 PERV pol 프라이머를 사용한 HEK293 세포에서의 PERV DNA 요소의 검출을 도시한다.

도 23A-23D (S20)는 PERV env 프라이머를 사용한 HEK293 세포에서의 PERV DNA 요소의 검출을 도시한다.

도 24A-24D (S21)는 PERV gag 프라이머를 사용한 HEK293 세포에서의 PERV DNA 요소의 검출을 도시한다.

도 25A-25B (S22)는 고도로 및 저도로 변형된 클론에서의 Cas9/2gRNA 발현 수준을 도시한다.

도 26 (S23)은 고도로 및 저도로 변형된 PK15 클론의 주요 성분 분석을 도시한다.

도 27A-27B (S24)는 유전자 세트 풍부화 분석을 도시한다.

도 28 (S25)은 고도로 변형된 클론 중에서의 indel 조성 분석 및 비교를 도시한다.

도 29A-29D (S26)는 활성 PERV 요소의 Cas9 제거를 초래하는 DNA 복구 프로세스의 마르코프(Markov) 모델 분석을 도시한다.

도 30 (S27)은 전체 게놈 시퀀싱 (WGS)을 사용한 오프-타겟 분석을 도시한다.

발명을 실시하기 위한 구체적인 내용

[0031] 본 발명의 측면은 핵산 조작을 위한 CRISPR/Cas9의 용도에 관한 것이다. 다중 돌연변이된 유전자를 운반하는 동물 (예를 들어, 돼지)의 생성을 위한 효율적인 기술의 개발이 본원에 기재된다. 구체적으로, 본원에서 CRISPR/Cas 시스템으로 치징되는, 규칙적 간격으로 군발하는 짧은 회문구조 반복서열 (CRISPR) 및 CRISPR 연관된 유전자 (Cas 유전자)는 예를 들어 다중화 게놈 편집을 위한 효율적인 유전자 표적화 기술로서 적응되었다. CRISPR/Cas 매개된 유전자 편집은 돼지 신장 상피 세포주 (예를 들어, PK15)에서 돼지 내인성 레트로바이러스 (PERV) *pol* 유전자의 62개 카피의 동시 불활성화를 고효율로 허용함이 본원에서 입증된다. PERV를 세포 내로 표적화하는 Cas9 mRNA 및 가이드 RNA (gRNA)의 공동-주입 또는 형질감염은 100%까지의 효율로 둘 다의 유전자에서 이중대립유전자 돌연변이를 갖는 인간 세포에의 PERV 전파의 1000배 초과를 생성하였다. CRISPR/Cas 시스템은 PERV의 모든 카피의 불활성화를 운반하는 세포의 1단계 생성을 허용함이 본원에서 보여진다. 특정 실시양태에서, 본원에 기재된 방법은 20% 내지 100%, 예를 들어, 적어도 20%, 30%, 40%, 50%, 60%, 70%, 80%, 85%, 90%, 95%, 또는 그 초과, 예를 들어, 최대 96%, 97%, 98%, 99%, 또는 그 초과를 효율로 1, 2, 3, 4, 5개, 또는 그 초과를 유전자의 불활성화를 갖는 세포 및 동물, 예를 들어, 돼지를 생성한다.

[0032] 실시예

[0033] 실시예 1. 돼지 내인성 레트로바이러스 (PERV)의 게놈-전체 불활성화

[0034] 이식용 장기의 부족은 장기 부전의 치료에 대한 주요한 장벽이다. 돼지 장기는 유망한 것으로 간주되지만, 그들의 사용은 인간에의 돼지 내인성 레트로바이러스 (PERV)의 전파에 관한 문제에 의해 점검되었다. 여기서 돼지 신장 상피 세포주 (PK15)에서의 모든 PERV의 박멸을 수행하였다. 먼저, PK15 PERV 카피 수는 62인 것으로 측정되었다. CRISPR-Cas9를 사용하여, PERV *pol* 유전자의 모든 62개 카피를 파괴하고, 본 발명자들의 조작된 세포를 사용하여 인간 세포에의 PERV 전파의 > 1000배 감소를 입증하였다. 이러한 연구는 CRISPR-Cas9 다중화 능력이 62만큼 높을 수 있음을 보였으며, PERV가 돼지-대-인간 이종이식에 대한 임상적 적용을 위해 불활성화될 수 있는 가능성을 입증한다.

[0035] 돼지 게놈은 몇개 내지 몇십개 카피의 PERV 요소를 함유한다. 다른 인수공통 병원체와는 달리, PERV는 생물보안 교배에 의해 제거될 수 없다. 인간에의 PERV 전파의 위험을 감소시키기 위한 이전의 전략은 소 간섭 RNA (RNAi), 백신, 및 아연 손가락 뉴클레아제 및 TAL 이펙터 뉴클레아제를 사용한 PERV 제거를 포함하였지만, 이들은 제한된 성공을 가졌다. 여기서 CRISPR-Cas9 RNA-가이드된 뉴클레아제 시스템의 성공적인 사용은 PERV *pol* 유전자의 모든 카피를 불활성화시키고, 인간 세포의 PERV 감염성의 1000배 감소를 실행하는데 사용될 수 있다.

[0036] PERV를 특이적으로 표적화하는 Cas9 가이드 RNA (gRNA)를 설계하기 위해, 돼지에서 공개적으로 이용가능한 PERV 및 다른 내인성 레트로바이러스의 서열 (방법)을 분석하였다. PERV 요소의 별개 계통군 (도 1A)을 확인하였으며, 액적 디지털 PCR을 사용하여 PK15 세포에서 PERV의 62개 카피가 있는 것으로 측정되었다 (도 1B). PERV 상의 *pol* 유전자의 고도로 보존된 측매 중심을 표적화하는 2개의 Cas9 가이드 RNA (gRNA)를 설계하였다 (도 1C, 도 S1). *pol* 유전자 생성물은 역전사효소 (RT)로서 기능하며, 따라서 바이러스 복제 및 감염에 필수적이다. 이들 gRNA는 돼지 게놈에서 모든 PERV를 표적화하였지만, 다른 내인성 레트로바이러스 또는 다른 서열은 그렇지 않은 것으로 측정되었다 (방법).

[0037] 초기 실험은 Cas9 및 gRNA를 일시적으로 형질감염시킨 경우 비효율적인 PERV 편집을 나타내었다 (도 S2). 따라서, PiggyBac 트랜스포존 시스템을 사용하여 독시시클린-유도성 Cas9 및 2개의 gRNA를 PK15 세포의 게놈 내로 전달하였다 (도 S2-3). Cas9의 연속적 유도는 PERV의 증가된 표적화 빈도를 초래하였으며 (도 S5), 37%의 최대 표적화 빈도 (게놈당 ~23개 PERV 카피)는 제17일에 관찰되었다 (도 S5). 아마도 CRISPR-Cas9에 의한 비-특이적

DNA 손상의 독성으로 인해, 보다 높은 농도의 독시시클린 또는 연장된 인큐베이션 어느 것도 표적화 효율을 증가시키지 않았다 (도 S4,5). Cas9가 렌티바이러스 구축물을 사용하여 전달된 경우 유사한 경향이 관찰되었다 (도 S6). 최대 PERV 표적화 효율을 나타낸 세포주를 유전자형분석하였다. 2개의 gRNA 표적 부위에 집중된 455개의 상이한 삽입 및 결실 (indel) 사건 (도 2B)이 관찰되었다. indel 크기는 1 내지 148bp 범위였으며; indel의 80%는 작은 결실이었다 (<9bp). 초기 딥 시퀀싱 결과를 생어 시퀀싱으로 확인하였다 (도 S7).

[0038] 높은 PERV 표적화 효율을 갖는 PK15 세포로부터의 단일 세포를 유동 세포측정법을 사용하여 분류하고, 생성된 클론의 pol 로커스를 딥 시퀀싱을 통해 유전자형분석하였다. 반복가능한 이중모드 (도 2A, S8-9) 분포는, 클론의 ~10%는 높은 수준의 PERV 파괴 (97%-100%)를 나타내고, 나머지 클론은 낮은 수준의 편집 (<10%)을 나타내는 것으로 관찰되었다. 개별적 indel 사건을 이들 클론의 게놈에서 조사하였다 (도 2B, 도 S10-11). 고도로 편집된 클론 (클론 20, 100%; 클론 15, 100%; 클론 29, 100%; 클론 38, 97.37%)에 대해, 각각의 클론에서 단지 16-20개의 고유한 indel 패턴 (도 2B, S11)이 관찰되었다. 또한, 클론에 걸쳐 각각의 클론 내에 indel의 훨씬 더 높은 정도의 반복이 있었으며 (도 S25), 이는 이전에 돌연변이된 PERV 카피가 Cas9에 의해 절단된 야생형 PERV를 복구하기 위한 주형으로서 사용된 유전자 전환의 메커니즘을 시사한다 (도 2B, 도 S25). PERV 제거 동안의 DNA 복구의 수학적 모델링 (도 S26) 및 발현 데이터의 분석 (도 S22-24)은 이러한 가설을 뒷받침하였으며, 고도로 편집된 클론이 Cas9 및 gRNA가 고도로 발현된 세포로부터 유래되었음을 시사하였다.

[0039] 다음으로, 예상치 않은 게놈 재배열은 다중화 게놈 편집의 결과를 조사했을 때 발생하였다. 개별적 변형된 클론의 핵형분석 (도 S12-S14)은 관찰가능한 게놈 재배열이 없었음을 지시하였다. 의도된 gRNA 표적의 각각에 대해 기껏해야 2bp 미스매치를 갖는 11개의 독립적 게놈 로커스를 조사하였으며, 비-특이적 돌연변이는 관찰되지 않았다 (도 S27). 이는 본 발명자들의 다중화 Cas9-기재 게놈 조작 전략이 파멸적인 게놈 불안정성을 유발하지 않았음을 시사한다.

[0040] 마지막으로, 돼지 게놈에서 PERV pol의 모든 카피의 파괴가 돼지로부터 인간 세포로의 PERV의 시험관내 전파를 제거할 수 있는지를 조사하였다. 고도로 변형된 PK15 클론의 세포 배양 상청액에서의 RT 활성의 검출 (도 S15)은 관찰되지 않았으며, 이는 변형된 세포가 단지 최소량의 PERV 입자를 생성하였음을 시사한다. HEK 293 세포와 함께 WT 및 고도로 변형된 PK15 세포의 공동-배양을 인간 세포에의 PERV DNA의 전파에 대해 직접 시험하였다. PK15 WT 및 HEK 293 세포를 5일 및 7일 동안 공동-배양한 후 (도 S16-17), HEK 293 세포에서의 PERV pol, gag, 및 env 서열을 검출하였다 (도 3A). PERV 감염의 추정된 빈도는 대략 1000 PERV/1000 인간 세포였다 (도 3B). 그러나, > 97% PERV pol 표적화를 갖는 PK15 클론은 배경 수준과 유사한 PERV 감염의 1000배까지의 감소를 나타내었다 (도 3C). 이들 결과는 PK15 클론과의 접촉의 내력을 가진 HEK293 세포의 연속 희석액의 PCR 증폭으로 확인되었다 (도 3D, S18-21). 최소로 변형된 클론 40과 공동-배양된 집단으로부터 단리된 단일 HEK293 세포에서의 PERV는 일관되게 검출되었지만, 고도로 변형된 클론 20과 공동-배양된 집단으로부터의 100개의 인간 세포에서의 PERV는 뚜렷하게 검출할 수 없었다. 따라서, 조작된 PK15 세포의 PERV 감염성은 1000배까지 감소되었다.

[0041] 요약하면, PK15 세포에서의 PERV pol의 62개 카피가 성공적으로 표적화되었으며, 인간 세포에의 PERV의 크게 감소된 시험관내 전파를 입증하였다. 인간에의 생체내 PERV 전파는 입증되지 않았지만, PERV는 여전히 위험한 것으로 간주되며, 본 발명자들의 전략은 이를 완전히 제거할 수 있었다. 돼지 배아 줄기 세포가 존재하지 않기 때문에, 이러한 시스템은 1차 돼지 세포에서 개발되고, 체세포 핵 전달을 사용하여 동물 내로 클로닝될 필요가 있을 것이다. 더욱이, 현저한 게놈 재배열이 없는 단일 돼지 세포에서의 62개 로커스의 동시 Cas9 표적화가 달성되었다. 본 발명자들의 지식으로, 동시에 편집되는 것으로 이전에 보고된 게놈 부위의 최대 수는 6이었다. 따라서, 본 발명자들의 방법은 생물학적 유의성의 다른 반복적 영역을 편집하는 가능성을 열고 있다.

[0042] 실시예 2. 방법

[0043] PERV 카피 수 정량화: 액적 디지털 PCRTM PCR (ddPCRTM)을 사용하여 제조자의 지시서 (바이오-라드(Bio-Rad))에 따라 PERV의 카피 수를 정량화하였다. 간략하게, 배양된 세포로부터의 게놈 DNA (DN이지 블러드 & 티슈 키트(DNeasy Blood & Tissue Kit), 퀴아젠(Qiagen))을 정제하고, 50 ng 게놈 DNA를 MseI (10U)로 37°C에서 1시간 동안 소화시키고, 10 μ l 2X ddPCR 마스터 믹스, 1 μ l의 18 μ M 표적 프라이머 & 5 μ M 표적 프로브 (VIC), 1 μ l의 18 μ M 참조 프라이머 & 5 μ M 참조 프로브 (FAM), 5 ng 소화된 DNA, 및 물을 20 μ l의 총 부피로 갖는 ddPCR 반응물을 제조하였다. 프라이머 및 프로브의 서열 정보는 확장된 데이터 표 1에서 발견될 수 있다.

[0044] 방법

[0045] 표 1 - ddPCR 검정에 사용된 프라이머

명칭	서열
프라이머Pol1-FW	CGACTGCCCCAAGGGTTCAA (SEQ ID NO:1)
프라이머Pol2-FW	CCGACTGCCCCAAGAGTTCAA (SEQ ID NO:2)
프라이머Pol-RV	TCTCTCCTGCAAATCTGGGCC (SEQ ID NO:3)
프로브Pol	/56FAM/CACGTACTGGAGGAGGGTCACCTG (SEQ ID NO:4)
프라이머돼지_액틴_F	Taaccgatcctttcaagcattt (SEQ ID NO:5)
프라이머돼지_액틴_R	Tggtttcaaagcttgcata (SEQ ID NO:6)
프로브돼지_액틴	/5Hex/cgtgggatgcttctgagaaag (SEQ ID NO:7)
프라이머돼지_GAPDH_F	Cgcgatctaattgtctcttc (SEQ ID NO:8)
프라이머돼지_GAPDH_R	Ttactccgacctcaccat (SEQ ID NO:9)
프로브돼지_GAPDH	/5Hex/cagccgctccctgagacac (SEQ ID NO:10)

[0046]

[0047] CRISPR-Cas9 gRNA 설계: MUSCLE를 사용하여 돼지 게놈에서 발견된 245개의 내인성 레트로바이러스의 다중 서열 정렬을 수행하였다. 서열의 계통수를 작성하고, PERV를 포함한 계통군을 확인하였다 (도 1A 참조). R 라이브러리 해독기 (DECIPHER)를 사용하여 모든 PERV를 표적화하지만 다른 내인성 레트로바이러스 서열은 그렇지 않은 특이적 gRNA를 설계하였다.

[0048] 세포 배양: PK15를 10% 소 태아 혈청 (인비트로젠(Invitrogen)), 및 1% 페니실린/스트렙토마이신 (Pen/Strep, 인비트로젠)으로 보충된 돌베코 변형 이글 배지 (DMEM, 인비트로젠) 고 글루코스에서 유지하였다. 모든 세포를 습화된 인큐베이터에서 37°C 및 5% CO₂에서 유지하였다.

[0049] PiggyBac-Cas9/2gRNA 구축 및 세포주 확립: PiggyBac-Cas9/2gRNA 구축물은 왕(Wang) 등에 이전에 보고된 플라스미드로부터 유래된다 (2). 간략하게, U6-gRNA1-U6-gRNA2를 코딩하는 DNA 단편을 합성하고 (진위즈 (Genewiz)), 이를 PiggyBac-Cas9 구축물 내로 혼입하였다. PiggyBac-Cas9/2gRNA 통합을 갖는 PK15 세포주를 확립하기 위해, $5 \cdot 10^5$ 개의 PK15 세포를 4 μ g PiggyBac-Cas9/2gRNA 플라스미드 및 1 μ g 슈퍼 PiggyBac 트랜스포사제(Super PiggyBac Transposase) 플라스미드 (시스템 바이오사이언시스(System Biosciences))로 리포펙타민(Lipofectamine) 2000 (인비트로젠)을 사용하여 형질감염시켰다. 통합된 구축물을 운반하는 세포에 대해 풍부화하기 위해, 2 μ g/mL 퓨로마이신을 형질감염된 세포에 첨가하였다. 음성 대조군에 기초하여, 퓨로마이신을 야생형 PK15 세포에 적용하였으며, 선택은 3일에 완료된 것으로 측정되었다. 이후, PK15-PiggyBac 세포주를 2 μ g/mL 퓨로마이신과 함께 유지하였다. 2 μ g/ml 독시시클린을 적용하여 Cas9 발현을 유도하였다.

[0050] 렌티바이러스-Cas9/2gRNA 구축 및 세포주 확립: 렌티-Cas9/2gRNA 구축물은 이전에 보고된 플라스미드로부터 유래되었다 (3). U6-gRNA1-U6-gRNA2를 코딩하는 DNA 단편을 합성하고 (진위즈), 이를 렌티-Cas9-V2 내로 혼입하였다. 렌티-Cas9/2gRNA를 운반하는 렌티바이러스를 생성하기 위해, $\sim 5 \cdot 10^6$ 개의 293FT HEK 세포를 3 μ g 렌티-Cas9-gRNA 및 12 μ g 비라파워 렌티바이러스 패키징 믹스(ViraPower Lentiviral Packaging Mix) (인비트로젠)로 리포펙타민 2000을 사용하여 형질감염시켰다. 렌티바이러스 입자를 형질감염 후 72시간에 수집하고, 바이러스 역가를 렌티-X 고스틱스(Lenti-X GoStix) (타카라 클론테크(Takara Clontech))를 사용하여 측정하였다. $\sim 10^5$ 개의 렌티바이러스 입자 내지 $\sim 1 \cdot 10^6$ 개의 PK15 세포를 형질도입하고, 형질도입 후 5일에 형질도입된 세포를 풍부화하기 위하여 퓨로마이신에 의한 선택을 수행하였다. 그 후, PK15-렌티 세포주를 2 μ

g/mL 퓨로마이신과 함께 유지하였다.

[0051] 콜로니화된 및 단일 PK15 세포의 유전자형분석: PK15 배양물을 TrypLE (인비트로젠)를 사용하여 분리하고, 생존성 염료 ToPro-3 (인비트로젠)을 갖는 PK15 배지에 $1-2 \cdot 10^5$ 세포/ml의 농도로 재현탁시켰다. 살아있는 PK15 세포를 100 mm 노즐을 갖는 BD FACSAria II SORP UV (비디 바이오사이언시스(BD Biosciences))를 사용하여 멸균 조건 하에서 단일-세포 분류하였다. SSC-H 대 SSC-W 및 FSC-H 대 FSC-W 이중선 식별 게이트 및 엄격한 '0/32/16 단일-세포' 분류 마스크를 사용하여 웰당 하나 및 단지 하나의 세포가 분류되는 것을 보장하였다. 세포를 100 μ l PK15 배지를 함유하는 각각의 웰을 갖는 96-웰 플레이트에서 분류하였다. 분류 후, 플레이트를 70g에서 3분 동안 원심분리하였다. 콜로니 형성은 분류 후 7일에 나타났으며, 유전자형분석 실험은 FACS 후 2주에 수행하였다.

[0052] 클론 확장 없이 단일 PK15 세포를 유전자형분석하기 위해, PERV 로커스를 이전에 보고된 단일 세포 유전자형분석 프로토콜에 따라 분류된 단일 세포로부터 직접 증폭시켰다 (4). 간략하게, 분류 전에, 모든 플라스틱 및 비-생물학적 완충제를 UV 방사선으로 30분 동안 처리하였다. 단일 세포를 0.5 μ l 10X 카파 고속 추출 완충제(카파 바이오시스템즈(KAPA Biosystems)), 0.1 μ l의 1U/ μ l 카파 고속 추출 효소 및 4.6 μ l 물을 운반하는 각각의 웰을 갖는 96-웰 PCR 플레이트로 분류하였다. 용해 반응물을 75°C에서 15분 동안 인큐베이션하고, 반응물을 95°C에서 5분 동안 불활성화시켰다. 그 후, 모든 반응물을 12.5 μ l 2X 카파 2G 패스트 (카파 바이오시스템즈), 100 nM PERV 일루미나 프라이머 (방법 표 2), 및 7.5 μ l 물을 함유하는 25 μ l PCR 반응물에 첨가하였다. 반응물을 95°C에서 3분 동안 인큐베이션한 후, 95°C, 10초; 65°C, 20초 및 72°C, 20초의 25 주기로 처리하였다. 일루미나 서열 어댑터를 첨가하기 위해, 5 μ l의 반응 생성물을 그 후 12.5 ml의 2 카파 하이파이 핫스타트 레디믹스(KAPA HIFI Hotstart Readymix) (카파 바이오시스템즈), 일루미나 서열 어댑터를 운반하는 100 nM 프라이머 및 7 μ l 물을 함유하는 20 μ l의 PCR 믹스에 첨가하였다. 반응물을 95°C에서 5분 동안 인큐베이션한 후, 98°C, 20초; 65°C, 20초 및 72°C, 20초의 15-25 주기로 처리하였다. PCR 생성물을 EX 2% 젤 (인비트로젠) 상에서 점검한 후, 300-400bp 생성물을 겔로부터 회수하였다. 그 후, 이들 생성물을 대략 동일한 양으로 혼합하고, 정제하고 (퀴아퀵 겔 엑스트랙션 키트(QIAquick Gel Extraction Kit)), MiSeq 퍼스널 시퀀서(Personal Sequencer) (일루미나)로 시퀀싱하였다. 딥 시퀀싱 데이터를 분석하고, CRISPR-GA를 사용하여 PERV 편집 효율을 측정하였다 (5).

[0053] 표 2. PERV pol 유전자형분석에 사용된 프라이머

명칭	서열
일루미나_프라이머Pol1	ACACTCTTTCCCTACACGACGCTCTTCCGATCTCGACTGCCCC AAGGGTTCAA (SEQ ID NO:11)
일루미나_프라이머Pol2	ACACTCTTTCCCTACACGACGCTCTTCCGATCTCCGACTGCCCC CAAGAGTTCAA (SEQ ID NO:12)
일루미나_프라이머Po3	GTGACTGGAGTTTCAGACGTGTGCTCTTCCGATCTTCTCTCCTG CAAATCTGGGCC (SEQ ID NO:13)

[0054]

[0055] 표적화 효율 추정: PERV 불활성화의 효율을 추정하기 위한 주문제작 파이프라인을 제작하였다. 간략하게, pol 유전자를 증폭시키고, PE250 또는 PE300을 사용한 일루미나 차세대 시퀀싱을 통해 시퀀싱하였다. 먼저, 2개의 중첩하는 판독물을 PEAR을 사용하여 합하고 (6), BLAT를 사용하여 참조 영역에 맵핑하였다. 맵핑 후, 판독물을 반수체형 (확장된 데이터 도 7 참조), 및 indel 유형의 특이적 조합을 함유하는 세트로 그룹화하였다. 맵핑된 판독물의 총 수의 0.5% 미만의 표시를 갖는 판독물 세트를 버렸다. 마지막으로, 귀엘(Gue11) 등에 기재된 바와 같이 상이한 삽입 및 결실을 지칭하기 위해 맵핑 산출량을 분석하였다 (5).

[0056] RNA-seq 분석: susScr3 돼지 게놈 및 Ensembl 전사체를 UCSC 게놈 브라우저 데이터베이스(Genome Brower Database)로부터 얻었다. RNA-Seq 판독물을 STAR 소프트웨어를 사용하여 참조 게놈에 맵핑하고 (7), 전사체의 RPKM을 BEDtools를 사용하여 정량화하였다 (8). 차등적 발현 분석을 R에서 DESeq2 패키지를 사용하여 수행하고 (9), 유전자 세트 풍부화 분석을 GSEA 소프트웨어에 의해 수행하였으며 (10), 유전자 세트 정의는 소프트웨어의

웹사이트로부터 얻었다.

- [0057] 역전사효소 (RT) 검정: PK15 세포 및 변형된 PK15 클론 (4개의 고도로 및 1개의 저도로 변형된 클론)의 RT 활성을 시험하기 위해, $5 \cdot 10^5$ 개의 세포를 $T75 \text{ cm}^2$ 플라스크에 플레이트팅하고, 시딩 후 4일에 상청액을 수집하였다. 배지를 $0.45 \text{ }\mu\text{M}$ 밀렉스(Millex)-HV 시린지 필터 (이엠디 밀리포어 코포레이션(EMD Millipore Corporation))를 사용하여 여과하고, 여과된 상청액을 4000g에서 30분 동안 아미콘 울트라(Amicon Ultra)-15 원심분리 필터 유닛 (이엠디 밀리포어 코포레이션)을 사용하여 농축시켰다. 농축된 상청액을 50,000 rpm에서 60분 동안 초원심분리하였다. 상청액을 주의깊게 제거하고, 바이러스 펠릿을 수집하고, 20 μl 의 10% NP40으로 37°C에서 60분 동안 용해시켰다.
- [0058] RT 반응을 옴미스크립트 RT 키트(Omniscrypt RT Kit) (퀴아젠)를 사용하여 수행하였다. 반응물의 총 부피는 20 μl 였으며, 이는 1X RT 완충제, 0.5 mM dNTP, 0.5 μM 인플루엔자 역방향 프라이머 (5' CTGCATGACCAGGGTTTATG 3') (서열식별번호: 14), 100 유닛의 RnaseOUT (라이프 테크놀로지(Life Technology)), 인비트로젠), 100 유닛의 슈퍼Rnase 억제제 (라이프 테크놀로지), 5 μl 의 샘플 용해물 및 5' 및 3' 말단 둘 다에서 rnase 저항성인 40 ng의 IDT-합성된 인플루엔자 RNA 주형을 함유하였다. RNA 주형 서열은 5' rA*rA*rC*rA*rU*rGrGrArArCrCrUrUrUrGrGrCrCrUrGrUrUrCrArUrUrUrArGrArArArUrCrArArGrUrCrArArGrArUrArCrGrCrArGrArGrArGrUrArGrArCrArUrArArArCrCrUrGrGrUrCrArUrGrCrArGrArCrCrU*rC*rA*rG*rU*rG 3' (* 포스포디에스테르 결합) (서열식별번호: 15)이었다. RT 반응이 완료된 후, RT 생성물을 PCR에 의해 인플루엔자 정방향 (5' ACCTTTGGCCCTGTTCATTT 3') (서열식별번호: 16) 및 인플루엔자 역방향 프라이머 (상기와 같이 나타난 서열)를 사용하여 조사하였다. 앰플리콘의 예상된 크기는 72bp였다.
- [0059] 감염성 검정
- [0060] HEK293-GFP 세포주 확립: 렌티-GFP 구축물은 플라스미드 pLVX-IRES-ZsGreen1 (클론테크(Clontech). 카탈로그 번호 632187; PT4064-5)로부터 유래되었다. 렌티-GFP를 운반하는 렌티바이러스를 생성하기 위해, $\sim 5 \cdot 10^6$ 개의 293FT HEK 세포를 3 μg 의 pVX-ZsGreen 플라스미드 및 12 μg 의 비라파워 렌티바이러스 패키징 믹스 (인비트로젠)로 리포펙타민 2000 (인비트로젠)을 사용하여 형질감염시켰다. 렌티바이러스 입자를 형질감염 후 72시간에 수집하고, 바이러스 역가를 렌티-X 고스티스 (타카라 클론테크)를 사용하여 측정하였다. $\sim 10^5$ 개의 렌티바이러스 입자 내지 $\sim 1 \cdot 10^6$ 개의 HEK293 세포를 형질감염시키고, 형질도입 후 5일에 형질도입된 세포를 풍부화하기 위해 퓨로마이신에 의한 선택을 수행하였다. 그 후, 293-GFP-렌티 세포주를 0.5 $\mu\text{g}/\text{mL}$ 퓨로마이신과 함께 유지하였다.
- [0061] HEK293-GFP에 대한 PK15 WT의 감염성 시험: $1 \cdot 10^5$ 개의 세포의 렌티-GFP-293FT HEK 세포 및 $1 \cdot 10^5$ 개의 PK15 WT 세포를 6-웰 플레이트에서 함께 배양하였다. 병행하여, $2 \cdot 10^5$ 개의 PK15 WT 세포를 대조군으로서 또 다른 웰에서 단독으로 배양하였다. 퓨로마이신 선택 실험을, 5 $\mu\text{g}/\text{mL}$ 의 항생제를 7일 동안 첨가함으로써 수행하였다. 렌티-GFP-293FT 인간 세포를 정제하기 위한 퓨로마이신 선택이 완료된 시점으로서, 대조군 웰에 생존성 세포가 없고, 실험 웰에 대략 100% GFP 양성 세포가 있는 시점을 측정하였다. 293FT HEK/PK15 WT 공동-배양으로부터의 세포를 상이한 기간에 수집하였다. 게놈 DNA를 (DN이지 블러드 & 티슈 키트, 퀴아젠)을 사용하여 293-GFP WT, PK15 WT의 배양된 세포 및 공동-배양된 세포로부터 추출하였다. 게놈 DNA 농도를 큐비트(Qubit) 2.0 형광계 (인비트로젠)를 사용하여 측정하고, 각각의 샘플로부터의 3 ng을 PCR을 위한 DNA 주형으로서 사용하였다. 모두 합쳐, 1 μL 의 게놈 DNA를 방법 표 3에 열거된 바와 같이 12.5 μL 2X 카파 하이파이 핫스타트 레드믹스 (카파 바이오시스템즈) 및 100 μM 의 프라이머를 함유하는 25 μL 의 PCR 믹스에 첨가하였다. 반응물을 95°C에서 5분 동안 인큐베이션한 후, 98°C, 20초; 65°C, 20초 및 72°C, 20초의 35 주기로 처리하였다. PCR 생성물을 EX 2% 겔 (인비트로젠) 상에서 가시화하고, 300-400개 염기 쌍의 밴드에 대해 관찰하였다.

[0062] 표 3 - 감염성 검정에 사용된 프라이머를 나타내는 표

명칭	서열
PERV <i>pol</i> -정방향	GGG AGT GGG ACG GGT AAC CCA (SEQ ID NO:17)
PERV <i>pol</i> -역방향	GCC CAG GCT TGG GGA AAC TG (SEQ ID NO:18)
PERV <i>env</i> -정방향	ACC TCT TCT TGT TGG CTT TG (SEQ ID NO:19)
PERV <i>env</i> -역방향	CAA AGG TGT TGG TGG GAT GG (SEQ ID NO:20)
PERV <i>gag</i> -정방향	CGC ACA CTG GTC CTT GTC GAG (SEQ ID NO:21)
PERV <i>gag</i> -역방향	TGA TCT AGT GAG AGA GGC AGA G (SEQ ID NO:22)
돼지 GGTA1 -정방향	GGA GCC CTT AGG GAC CAT TA (SEQ ID NO:23)
돼지 GGTA1 -역방향	GCG CTA AGG AGT GCG TTC TA (SEQ ID NO:24)
인간 ACTB-정방향	GCC TTC CTT CCT GGG CAT GG (SEQ ID NO:25)
인간 ACTB-역방향	GAG TAC TTG CGC TCA GGA GG (SEQ ID NO:26)

[0063]

[0064]

HEK293-GFP 세포에서 감염된 PERV 카피 수의 정량화: qPCR을 수행하여 HEK293-GFP 세포에서 PERV 카피 수를 정량화하였다. 상이한 양의 PK15 WT 세포의 게놈 DNA를 qPCR 반응을 위한 주형으로서 사용하였다. 반응을 카파 SYBR 패스트 qPCR 마스터 믹스 유니버설 (카파 바이오시스템즈)을 사용하여 삼중으로 수행하였다. PERV *pol*, *env*, *gag* 프라이머, 인간 ACTB 및 돼지 GGTA1 프라이머 (방법 표 3)를 1 μ M의 최종 농도로 첨가하였다. 반응물을 95°C에서 3분 동안 인큐베이션한 후 (효소 활성화), 95°C, 5초 (변성); 60°C, 60초 (어닐링/연장)의 50 주기로 처리하였다. 게놈 DNA 양의 로그는 정량화 주기 (Cq)로 선형화한다. *pol*, *gag*, *env* 프라이머를 사용하여 PERV의 존재에 대해 조사하였다. 돼지 GGTA1 프라이머는 감염 후 인간 세포에서 잠재적 돼지 게놈 오염물에 대해 제어하는 기능을 하였다. 모든 실험은 삼중으로 수행하였다.

[0065]

HEK293-GFP에 대한 변형된 PK15 클론의 감염성 검정: $1 \cdot 10^5$ 개의 세포의 HEK293-GFP 세포 및 $1 \cdot 10^5$ 개의 세포의 고도로 변형된 (15, 20, 29, 38) 클론 및 저도로 변형된 클론 (40, 41)을 6-웰 플레이트에서 7일 동안 공동-배양하였다. PERV 요소에 대해 조사하기 위해 HEK293-GFP 세포를 단리하기 위해, GFP 양성 세포를 이중 분류하여 인간 세포 집단을 정제하였다.

[0066]

HEK293-GFP 세포에 대한 상이한 클론의 PERV 감염성을 정량화하기 위해, qPCR 검정 및 PCR 검정 둘 다를 분류 후 연속 희석된 HEK293-GFP 세포 상에서 수행하였다. qPCR 검정을 위해, 게놈 DNA (DN이지 블러드 & 티슈 키트, 쿼아젠)를 이중 분류된 HEK293-GFP 세포로부터 추출하였다. 게놈 DNA 농도를 큐비트 2.0 형광계 (인비트로젠)를 사용하여 측정하였다. 모두 합쳐, 3 ng의 게놈 DNA를 20 μ L의 카파 SYBR FAST qPCR 반응물 (카파 바이오시스템즈)에 PERV *pol*, *env*, *gag* 및 돼지 GGTA 프라이머를 각각 사용하여 첨가하였다 (확장된 데이터 표

2). qPCR 절차를 상기 기재된 바와 같이 수행하였다. 연속 희석 검정을 위해, 정제된 HEK293-GFP 세포를 직접 게놈 DNA 추출 및 PCR 반응을 위해 96-웰 PCR 플레이트로 분류하였다 (1 세포/웰, 10 세포/웰, 100 세포/웰, 1000 세포/웰). 간략하게, 세포를 2 μ L의 10X 카파 고속 추출 완충제, 0.4 μ L의 1 U/ μ L 카파 고속 추출 효소 및 17.6 μ L의 PCR-등급 물 (카파 바이오시스템즈)을 포함하는 20 μ L 용해 반응물로 분류하였다. 그 후, 반응물을 55°C에서 10분 동안 (용해), 그 후 95°C에서 5분 동안 (효소 불활성화) 인큐베이션하였다. 이어서, PCR 마스터 믹스를 제조하였다. 모두 합쳐, 2 μ L의 게놈 DNA 용해물을 4개의 상이한 25 μ L의 카파 하이파이 핫스타트 PCR 반응물 (카파 바이오시스템즈)에 1 μ M PERV pol, env, gag 프라이머, 및 돼지 GGTA 프라이머를 각각 사용하여 첨가하였다 (확장된 데이터 표 2). 반응물을 95°C에서 3분 동안 인큐베이션한 후 (초기 변성), 95°C, 15초 (변성); 60°C, 15초 (어닐링), 72°C, 15초/kb, 그 후 75°C, 1분/kb (최종 연장)의 35 주기로 처리하였다. (카파 바이오시스템즈). PCR 생성물을 96 웰 E-겔® 아가로스 겔, SYBR® 세이프 DNA 겔 (인비트로젠) 상에서 가시화하였다.

[0067] CRISPR-Cas9 오프-타겟 분석: 전체 게놈 시퀀싱 (WGS) 데이터를 PK15 (비처리된 세포주) 및 클론 20 (고도로 편집된 클론)에 대해 얻었다. Cas9/2gRNA의 잠재적 오프-타겟 효과를 조사하기 위해, 참조 서열 (서스 스크로파 (Sus Scrofa) 10.2)을 2개의 gRNA에 의해 표적화된 20 bp 서열과는 단지 1 또는 2 bp만큼 상이한 부위에 대해 조사하였다. 11개의 이러한 부위를 확인하고, 이들을 200 bp의 그들의 이웃하는 영역과 함께 추출하였다 (도 S1). BLAT를 사용하여 WGS 판독물을 추출된 참조 서열에 맵핑하고, 오프-타겟 효과의 결과로서 클론 20에서 나타난 잠재적 indel 패턴에 대해 조사하였다. 로커스당 7-8 X의 평균 커버리지가 얻어졌다. 참조 서열과 <50 bp 매치를 갖는 판독물을 배제하였다. indel의 존재를 지시할 수 있는 다중 정렬 블록을 갖는 참조 서열에 맵핑된 판독물의 경우, 그의 정렬 블록이 <20 bp 매치를 함유한 판독물은 참조 서열로 배제되었다. 나머지 맵핑된 판독물을 검사한 후, 클론 20에 존재하는 임의의 오프-타겟 indel 패턴의 검출은 없었다. 여기서 오프-타겟에 대한 포괄적 조사에 대한 또 다른 도전은 서스 스크로파 게놈이 여전히 완료되지도 않고, 완전히 어셈블리되지도 않는 것이며, 이는 전체-게놈 분석을 수행하는 능력을 제한한다.

[0068] 누적 PERV 불활성화 동안 DNA 복구 프로세스 상호작용의 수학적 모델: 이러한 연구에서, PERV 요소를 Cas9에 의해 생성된 dsDNA 커트에 반응하여 DNA 복구 프로세스에 의해 생성된 돌연변이에 의해 불활성화시켰다. 일반적으로, dsDNA 커트는 비-상동 말단 연결 (NHEJ) 또는 상동 복구 (HR) 중 어느 하나에 의해 복구될 수 있으며, HR은 적합한 상동성 아암을 갖는 주형의 존재를 고려하여 커팅 부위에서 DNA 주형 서열의 정확한 카피를 생성할 수 있는 반면, NHEJ는 돌연변이 (특히 indel)를 생성할 수 있고, 종종 "오류 유발성"인 것으로 간주됨이 이해된다. 그러나, NHEJ는 또한 dsDNA 커트를 매우 정확하게 복구할 수 있다는 증거가 또한 있으며 (11, 12), 돌연변이된 vs. NHEJ에 의한 완벽한 복구의 상대적 비율은 결코 정확하게 측정되지 않았다. 특히, 효율적인 표적화된 뉴클레아제, 예컨대 Cas9가 오래 계속된 기간 동안 발현되는 경우, NHEJ 또는 HR 중 어느 하나에 의한 커팅 부위의 완벽한 복구는 다시 커팅될 수 있는 표적 부위를 재생성할 것이다. 타당한 가설은 완벽한 복구 및 재-커팅의 프로세스는 표적 부위를 인식하는 뉴클레아제의 능력을 파괴한 돌연변이가 발생할 때까지 반복적으로 일어날 것이라는 것이다. 이들 복구 양식이 PERV 제거의 과정 동안 함께 작용할 수 있는지를 탐구하기 위해, 마르코프 프로세스로서의 그들의 상호작용을 모델링하였다. 구체적으로, 하기와 같이 가정하였다:

[0069] • 세포에서 뉴클레아제 표적의 N개의 동일한 카피가 있다.

[0070] • 단지 야생형 표적만이 인식되고, 커팅되며, 한 번에 단지 1개의 표적만이 커팅되고, 복구된다.

[0071] • DNA 복구는 하기 중 어느 하나이다:

[0072] o NHEJ에 의한 표적 부위의 완벽한 복원 (확률 n으로)

[0073] o 표적 인식을 제거하는 돌연변이의 생성을 초래하는 NHEJ (확률 m으로)

[0074] o 세포에서 다른 N-1개의 표적 서열 중 어느 하나를 사용한 HR의 복구 (확률 h로)

[0075] 따라서, $n+m+h=1$ 이다.

[0076] 마르코프 모델은 확률 분포 $P^{(c)} = (P_0^{(c)}, P_1^{(c)}, \dots, P_N^{(c)})$ 을 산출하며, 여기서 $P_i^{(c)}$ 는 커트 c에서 i개의 표적-제거 돌연변이가 있을 확률이고, $c = 0, 1, 2 \dots$ 이다. 초기 조건 $P^{(0)} = (1, 0, \dots, 0)$, 즉, 모든 표적은 야생형으로서 시작하는 것으로 가정한다. $N+1 \times N+1$ 전이 행렬 M은 하기와 같이 주어진다.

$$\left. \begin{aligned} M(i, i) &= n + h \cdot \frac{N - i - 1}{N - 1} \\ M(i, i + 1) &= m + h \cdot \frac{i}{N - 1} \end{aligned} \right\} 0 \leq i < N \text{에 대해}$$

$$M(N, N) = 1 \quad i = N \text{에 대해}$$

$$M(i, j) = 0 \quad \text{모든 다른 } 0 \leq i, j \leq N \text{에 대해}$$

[0077]

[0078] 마지막으로, $P^{(c+1)} = P^{(c)}M$, $c = 0, 1, 2, \dots$ 에 대해

[0079] M에 대한 식은 상기 명제 ii를 가정하며, 수학적 용어로, 세포에서 돌연변이된 부위의 수가, 야생형 부위에서의 커트가 야생형 주형의 또 다른 카피를 사용하여 NHEJ에 의해 또는 HR에 의해 완전히 복구될 때는 언제나 변화하지 않고 남아있지만 ($M(i, i)$ 에 대한 식), 커트가 이전에 돌연변이된 부위를 사용하여 돌연변이유발 NHEJ에 의해 또는 HR에 의해 복구되는 경우는 1만큼 증가하는 것 ($M(i, i + 1)$ 에 대한 식)으로 진술한다.

[0080] 모델은 실제 생물학에 2가지 주목할 만한 단순화를 도입한다: (i) 표적 인식은 2항인 것으로 가정된다 - 뉴클레아제는 표적을 인식하거나, 그렇지 않거나 둘 중 하나이다. 이는 여전히 표적 인식을 뒷받침하는 작은 돌연변이가 야생형 커팅 속도를 실질적으로 변경시키지 않고, 따라서 야생형 부위와 함께 효과적으로 묶여질 수 있음을 가정하는 것에 버금간다. (ii) 돌연변이된 vs. 야생형 주형을 사용한 HR 복구는 동등하게 효율적인 것으로 가정된다. 이들 단순화를 다루기 위한 변형이 모델에 이루어질 수 있지만, 이는 여기서 고려되지 않는다. 또한, 공식적으로, 상기 가정 ii를 고려하면, c 의 일부 값에 대해 조건 $P_N^{(c)} = 1$ 이 도달되는 경우, 마르코프 프로세스는 사실상 중단되어야 하는데, 이는 이 시점에서 야생형 부위는 커팅되어 남아있는 반면, 수학적으로 대신 일어나는 것은 커팅이 계속되지만, 모델은 고정된 상태로 남아있기 때문이라는 것은 주목할 만한 가치가 있다. 마지막으로, 모델은 돌연변이 카운트 분포를 독립 변수 c (커트의 수)의 함수로서 효과적으로 나타내고, 시간의 함수로서는 아니다. 시간은 c 와 함께 단조적으로 증가하는 것으로 가정될 수 있지만, DNA 복구 또는 PERV 부위 제거의 시간 속도에 관한 예측은 이루어지지 않는다.

[0081] 마르코프 모델을 통한 PERV 제거를 분석하기 위해, N 은 항상 62로 설정되었다. 그러나, 완벽한 vs. 돌연변이유발 NHEJ 복구의 상대적 효율은 공지되어 있지 않기 때문에 (상기 언급된 바와 같음), 그리고 돌연변이유발 NHEJ vs. HR 복구의 상대적 속도는 세포 상태 및 유형에 따라 폭넓게 다양할 수 있기 때문에, n , m , 및 h 에 대한 모든 가능한 파라미터 값 (모두 합쳐 2500개 파라미터 조합)의 완전한 2-차원 공간을 커버하는 이산 그리드에 대한 돌연변이 카운트 분포를 산출하였다. 모델은 매트랩(MatLab) (매트웍스(Mathworks), 월섬(Waltham)) 스크립트 및 라이브러리 마르코프체인을 사용한 R 스크립트 (각각 보충 파일 모델마르코프.m, 모델마르코프.R로서 이용가능함) 둘 다로서 실행되었다.

[0082] 특정 파라미터 값에 대한 마르코프 모델을 통해 돌연변이 카운트 분포를 산출하는 것에 추가로, 매트랩 스크립트는 일련의 K 커트 전반에 걸쳐 NHEJ 및 HR 복구 프로세스의 무작위 시뮬레이션을 수행하였으며, 이는 도 27 B-C에 도시된, 총 돌연변이 vs. 별개 NHEJ 사건의 수의 이변량 분포가 추정되는 것을 허용한다. R 스크립트를 사용하여 상기 기재된 n , m , 및 h 조합의 그리드에 대한 시스템의 가장 가능성이 있는 상태를 추정하였다. K 는 산출에 따라 다양하였다. 도 S27에 도시된 바와 같이, 모델의 비가변적 결과는 그의 평균이 c 를 갖는 N 개의 돌연변이에서 고정을 향해 나아간 돌연변이 카운트의 단일모드 분포였으며, 도 S27 B-C에서, K 는 고정을 입증하기 위해 충분히 높은 값으로 설정하였다. n , m , 및 h 그리드에 대한 시스템의 가장 가능성이 있는 상태의 계산을 위해, K 는 50, 100, 200, 또는 500으로 설정하였으며, 각각의 파라미터 조합에 대해 100건의 시뮬레이션을 수행하였다.

[0083] 데이터 기탁

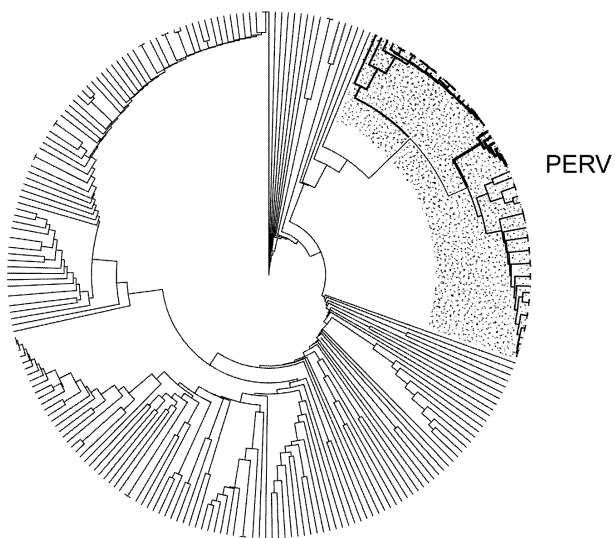
[0084] PERV 요소 유전자형분석 데이터를 갖는 일루미나 Miseq 데이터를 유럽 생물정보학 협회 (European Bioinformatics Institute) (EBI)에 의해 호스팅된 유럽 뉴클레오타이드 아카이브 (European Nucleotide Archive) (ENA)에 제출 참조번호 PRJEB11222로 업로드하였다.

- [0085] 부록 A는 본 교시사항의 다양한 측면에 관한 추가의 정보를 제공하며, 이는 그 전문이 본원에 참조로 포함된다.
- [0086] DNA 서열 목록은 추가로 돼지 게놈 서열로부터 및 공개 서열 데이터베이스로부터 추출된 다중 내인성 레트로바이러스 요소의 게놈 서열을 포함한다. (서열식별번호: 30-280)
- [0087] 본원에 인용된 모든 특허, 공개된 출원 및 참고문헌의 교시사항은 그 전문이 본원에 참조로 포함된다.
- [0088] 이 발명을 특히 그의 예시 실시양태를 참조로 나타내고 기재하였지만, 첨부된 청구범위에 의해 포함되는 본 발명의 범위로부터 벗어나지 않고 형태 및 상세사항에 다양한 변화가 그에 이루어질 수 있음은 관련 기술분야의 통상의 기술자에 의해 이해될 것이다.

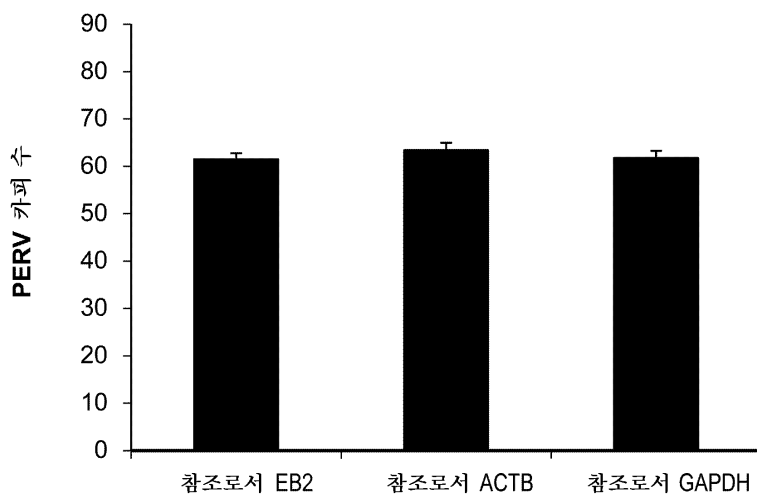
도면

도면1i

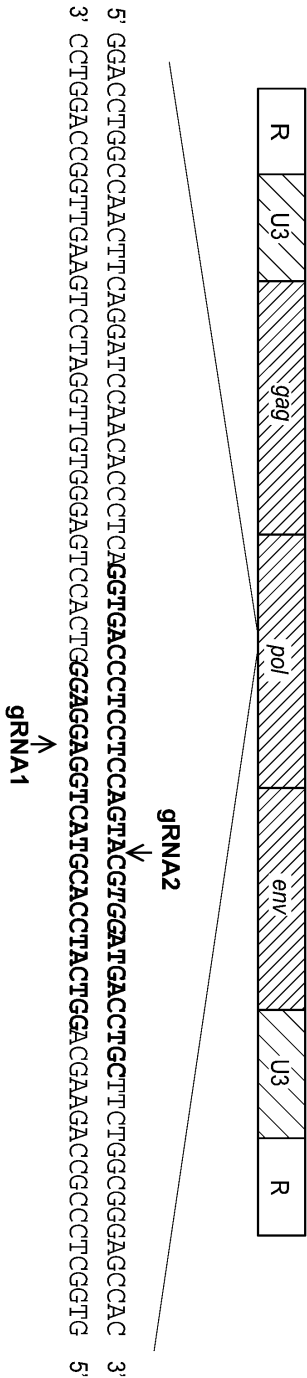
1A



1B

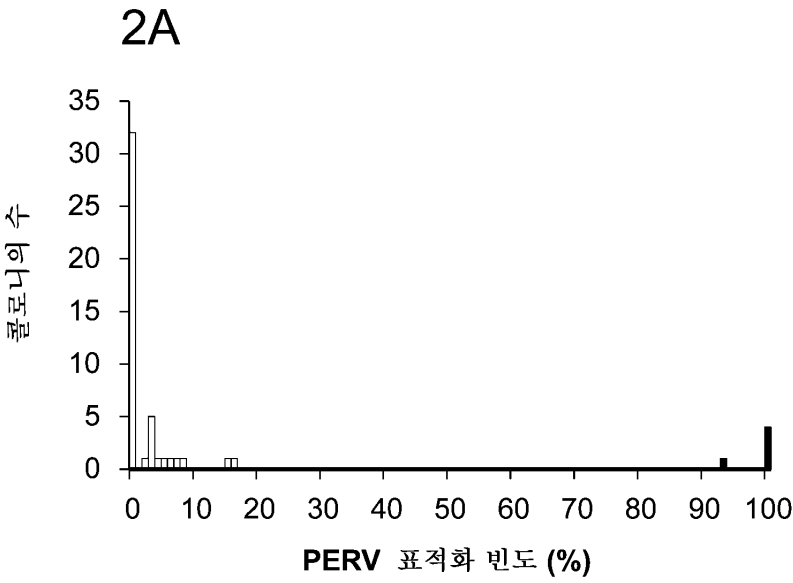


1C

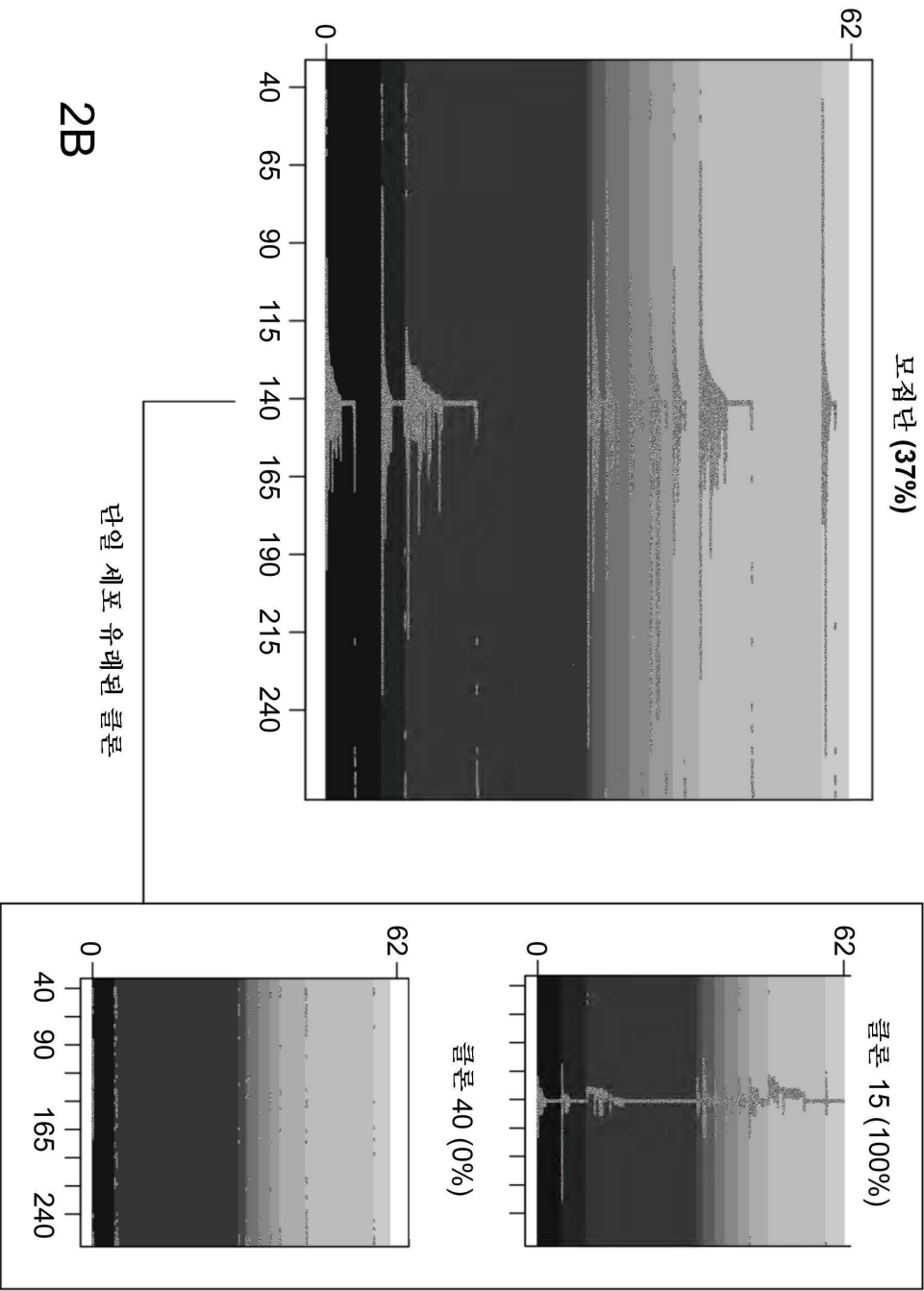


도면1ii

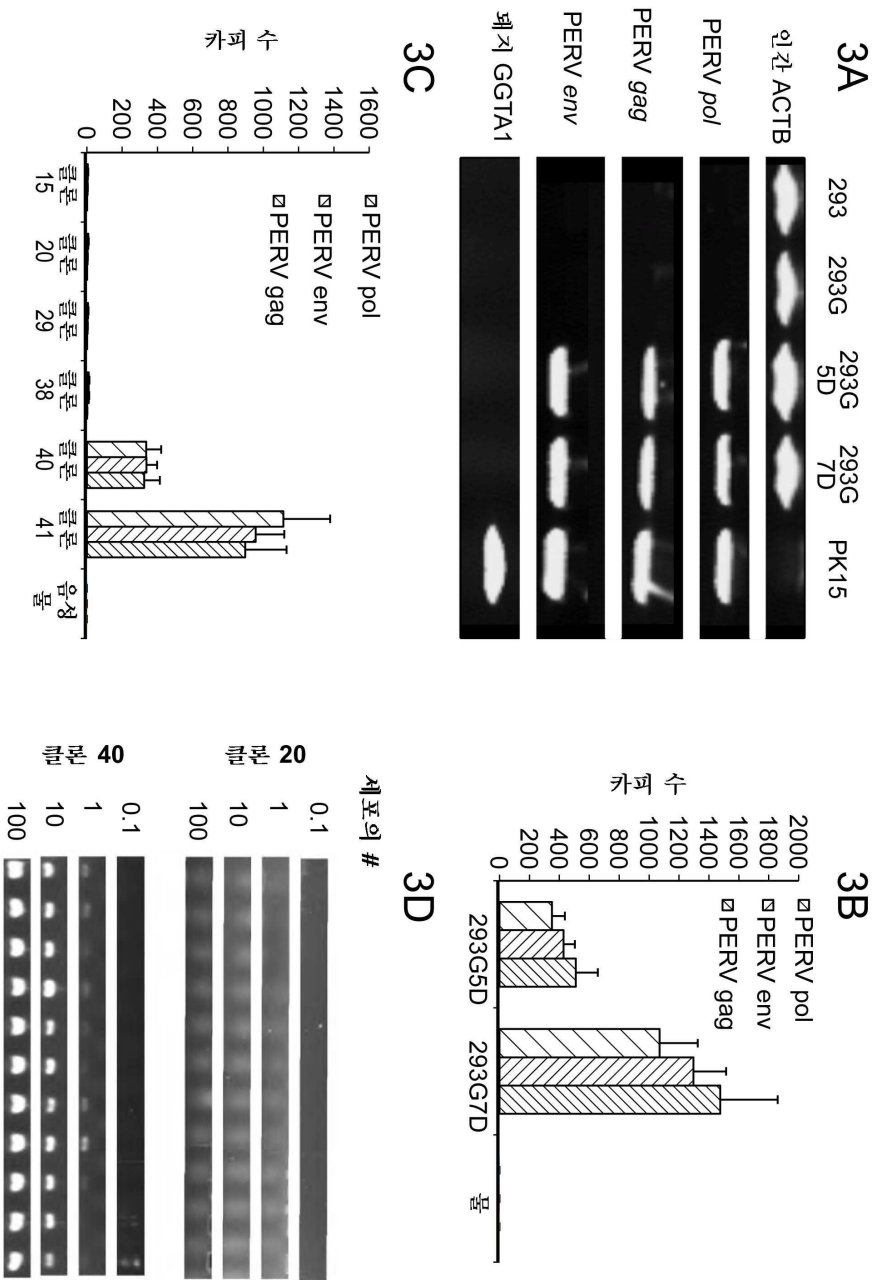
도면2i



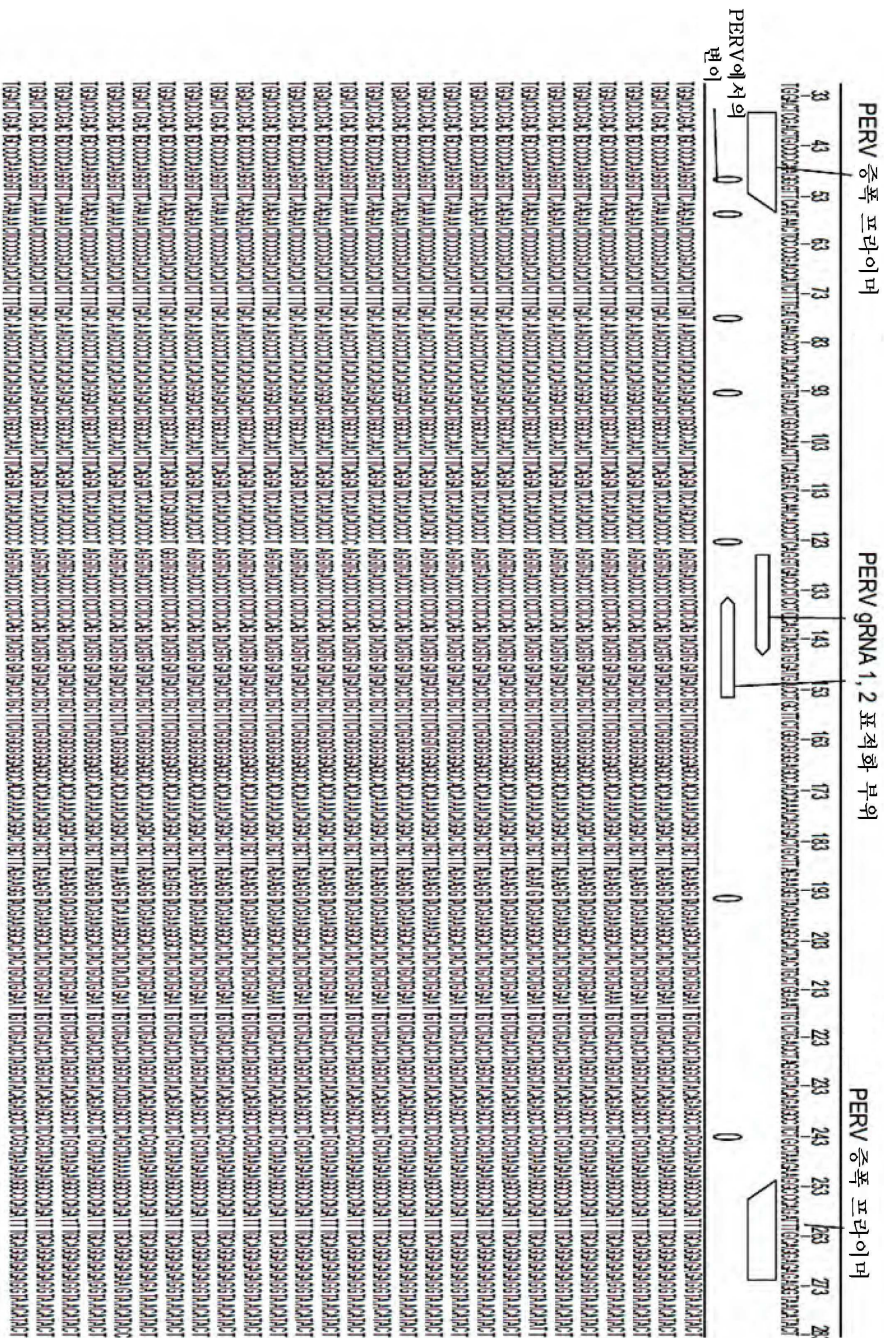
도면2ii



도면3



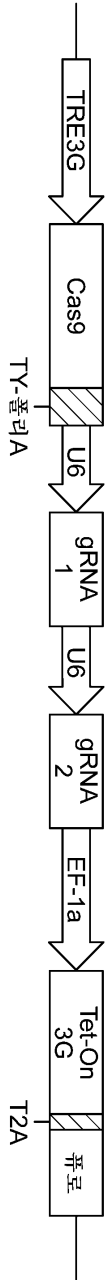
도면4i



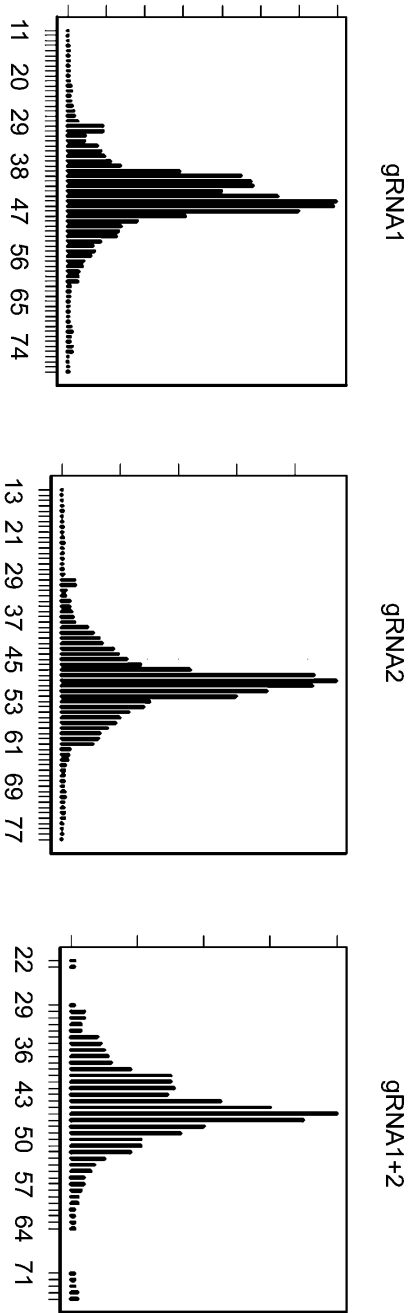
도면4*ii*



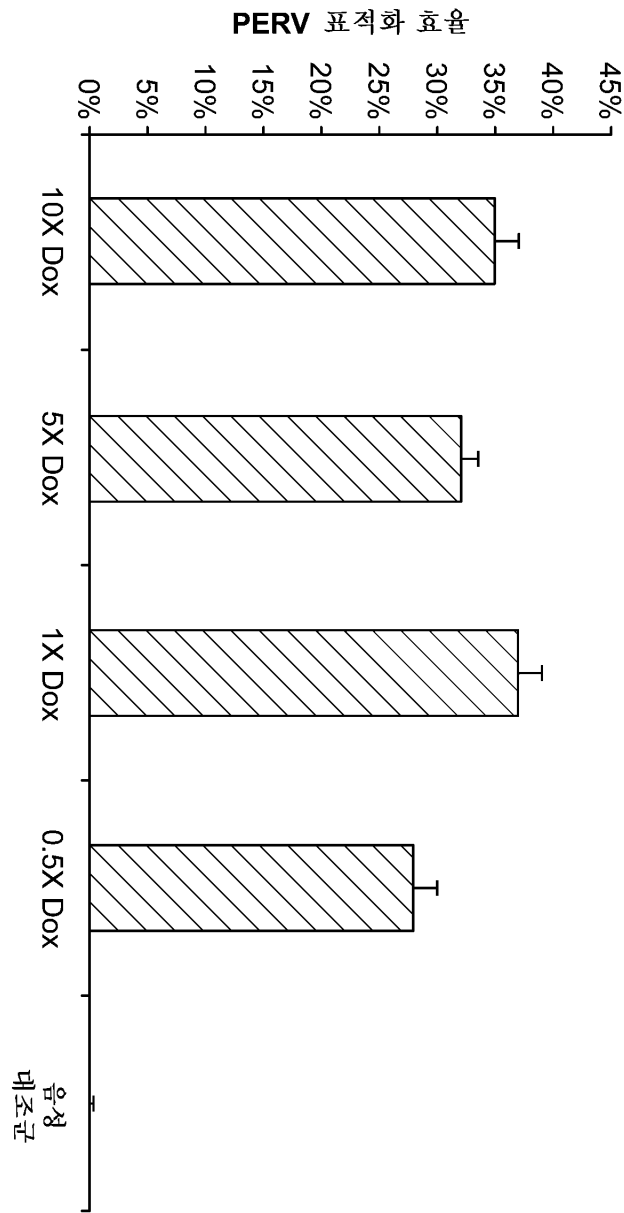
도면5



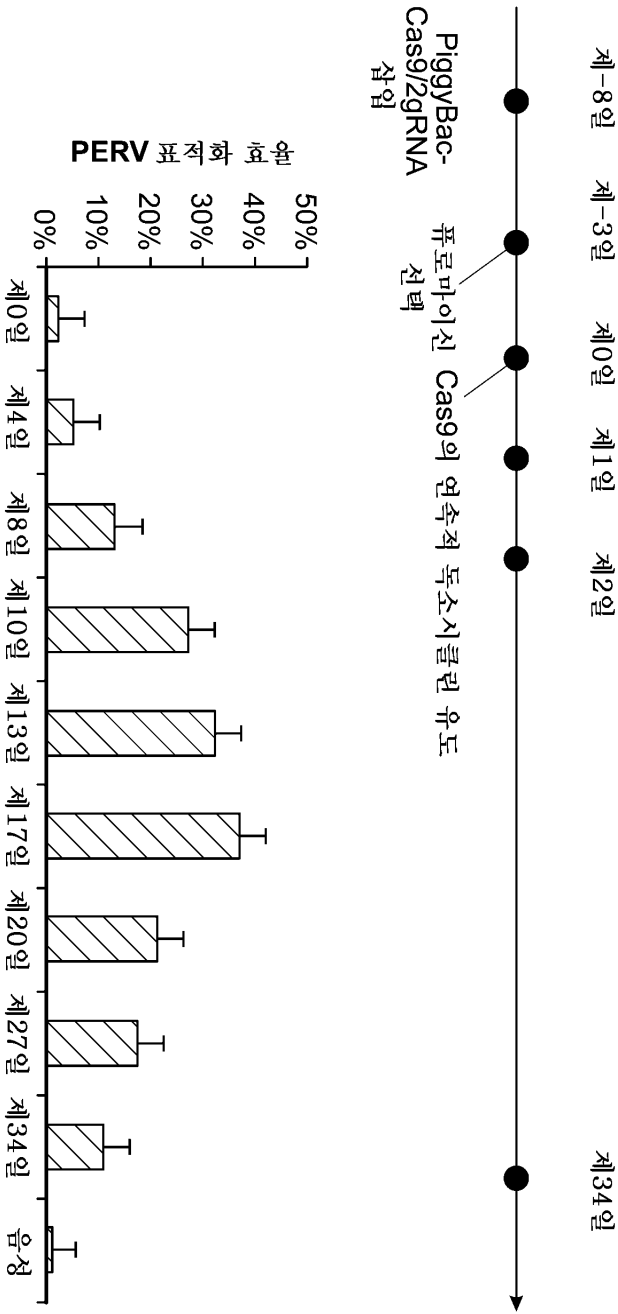
도면6



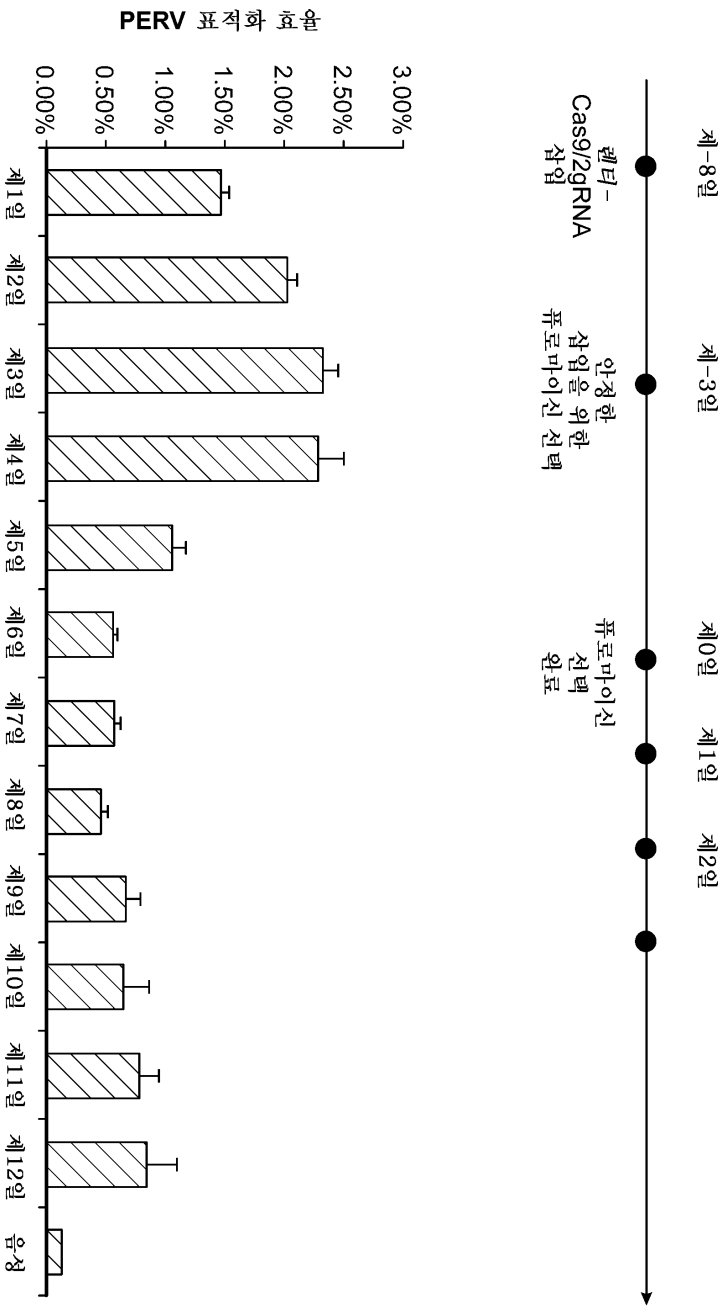
도면7



도면8



도면9



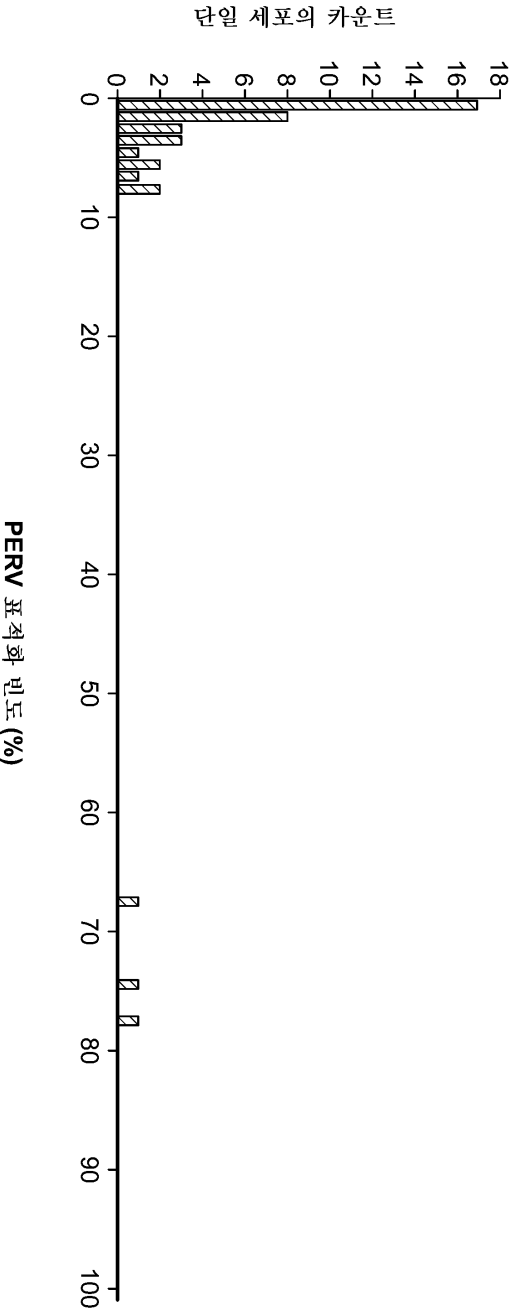
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5' GGACCTGGCCAACTTCAGGATCCAACACCCCTCAGGTGACCCCTCCT-CCAG-TACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACC-----A-C--AG-A-----G--A-----CCAG-TACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACCTGGCCAACTTCAGGATCCA-----G----C-----ACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACCTGGCCAACTTCAGGATCCAACACCCCTCAGGTGACCCCTCCT-CCA-----TGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACCTGGCCAACTTCAGGATCCAACACCCCTCAGGTGAC--CCT-CCAG-TACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACCTGGCCAACTTCAGGATCCAACACCCCTCAGGTGACCCCTCCT-CCAGTTACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'
5' GGACCTGGCCAACTTCAGGATCCAACACCCCTCAGGTGACCCCTCCAG-TACGTGATGACCTGCTTCTGGCGGGAGCCAC 3'

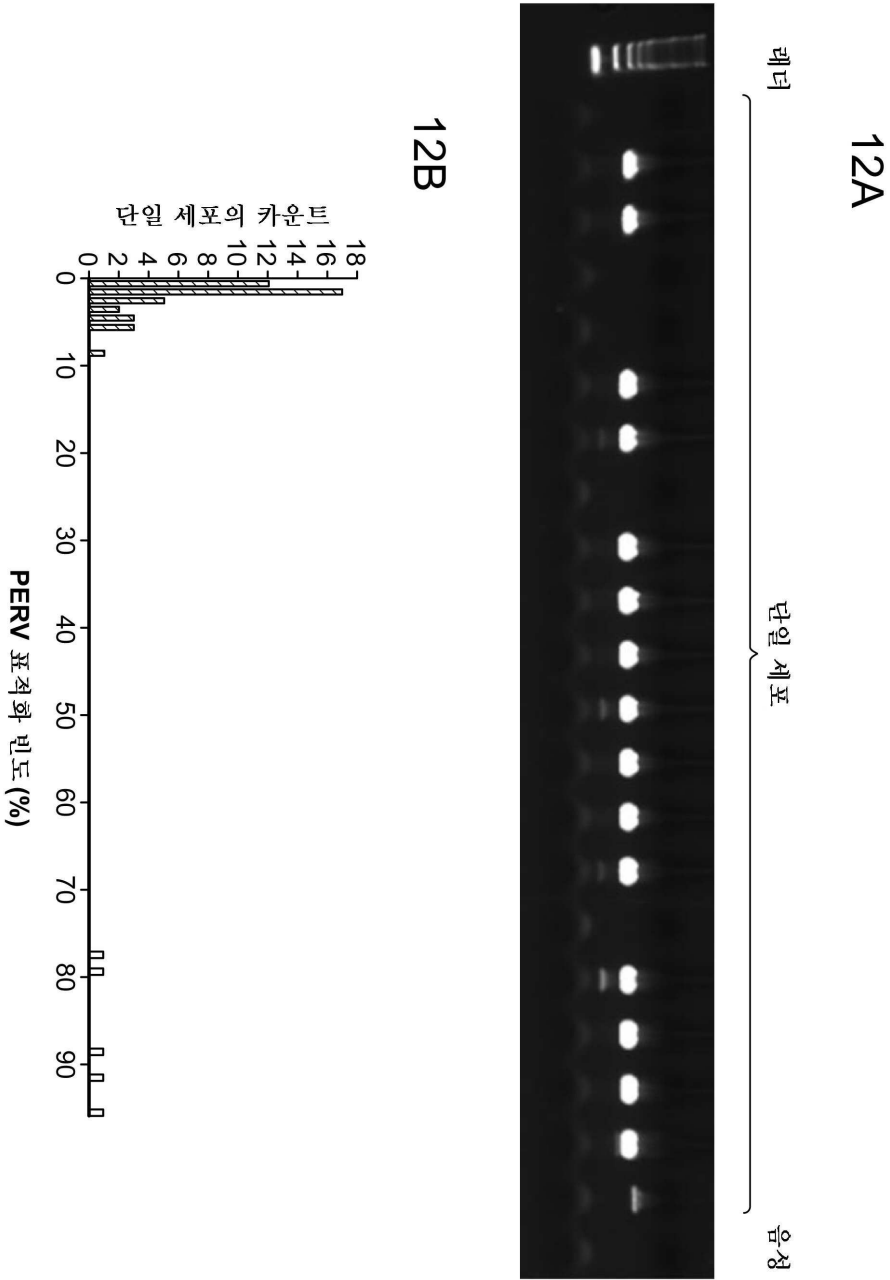
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도면10

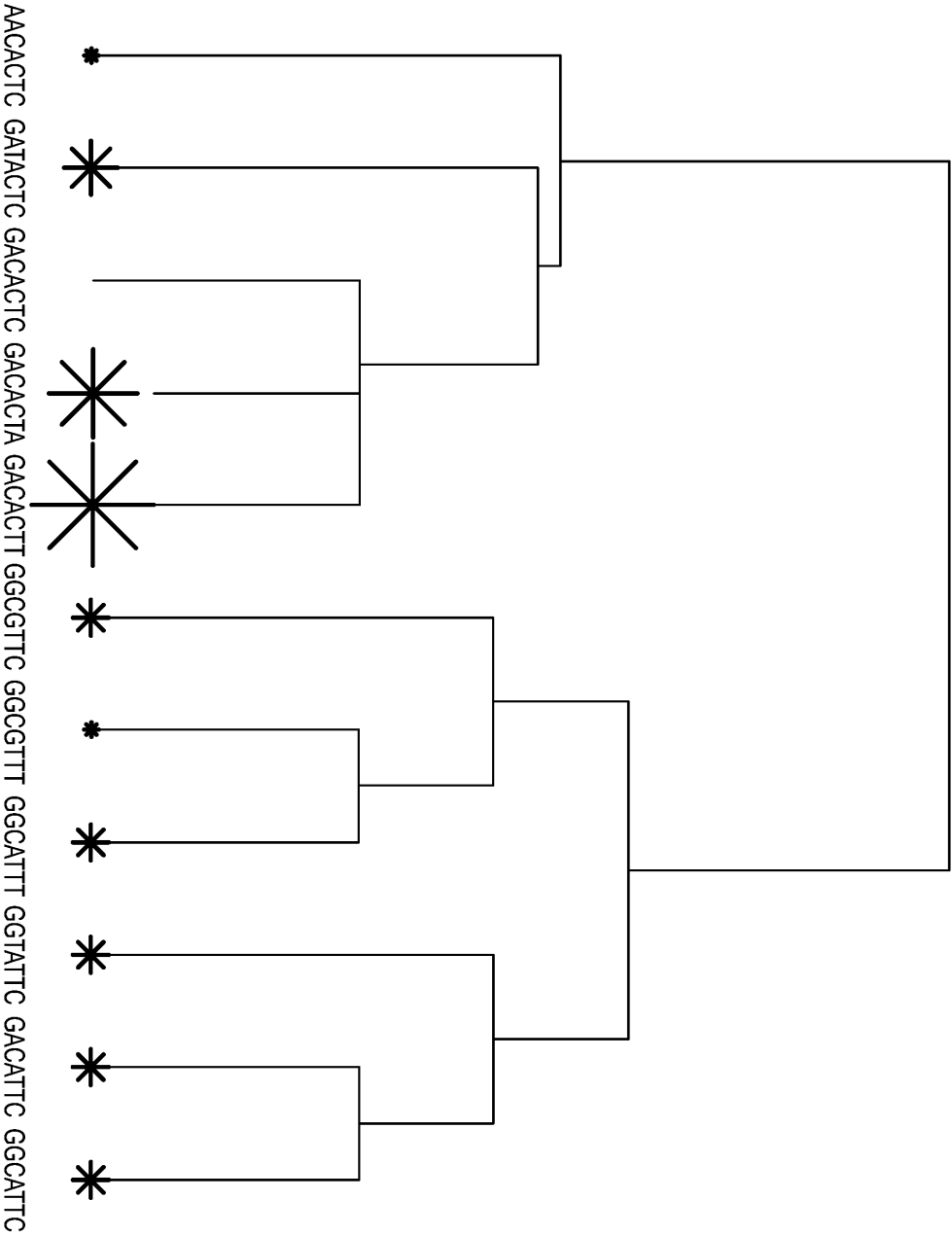
도면11

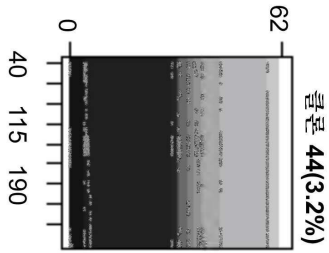
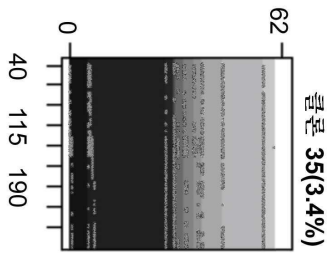
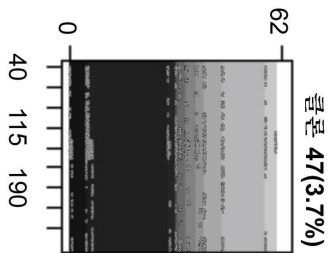
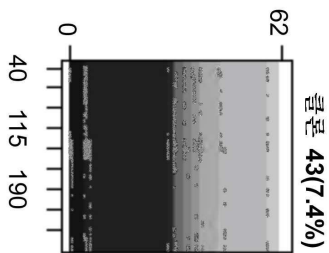
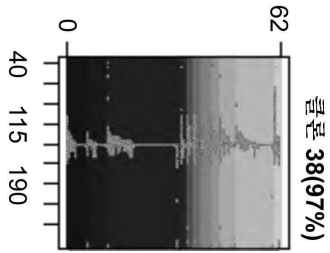
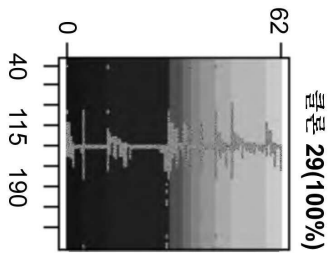
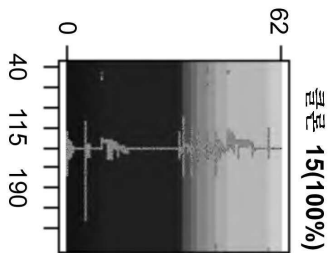
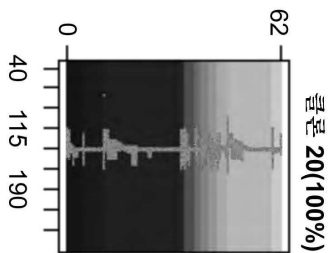


도면12



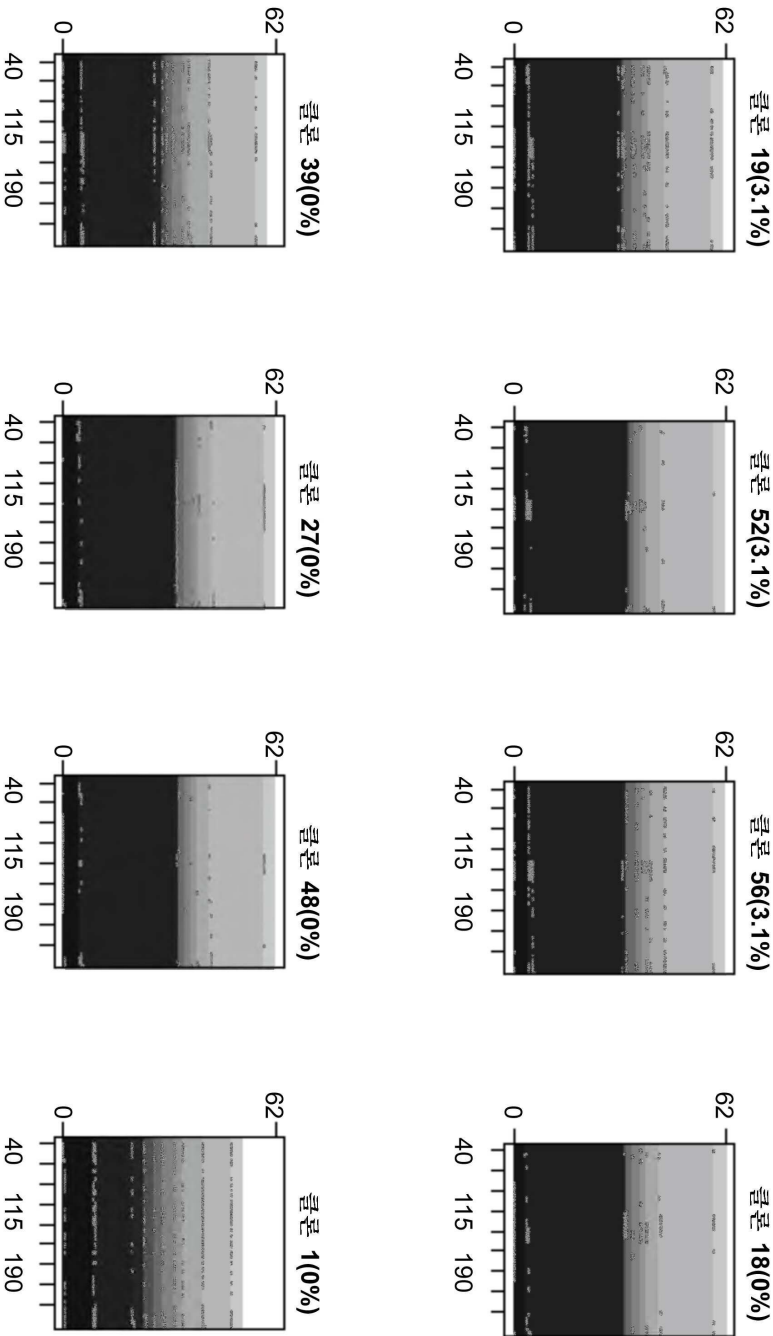
도면13

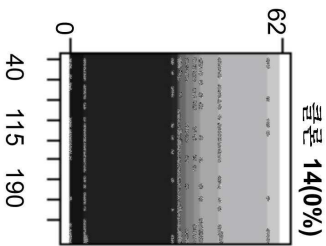
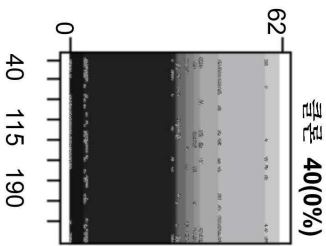
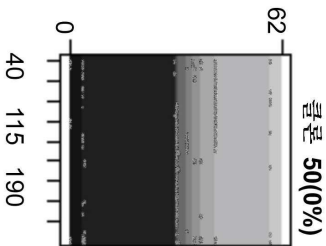
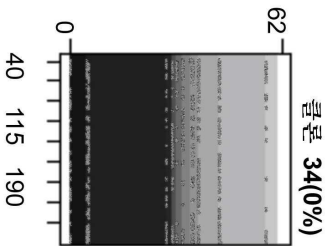
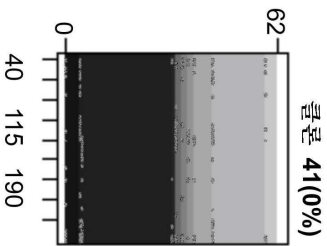
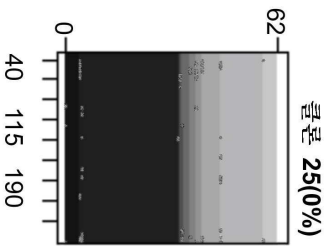
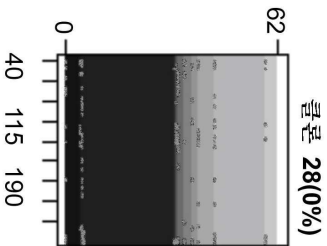
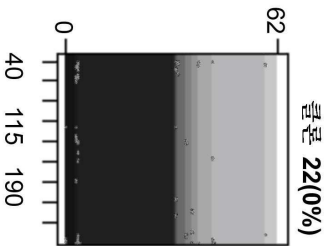




도면14i

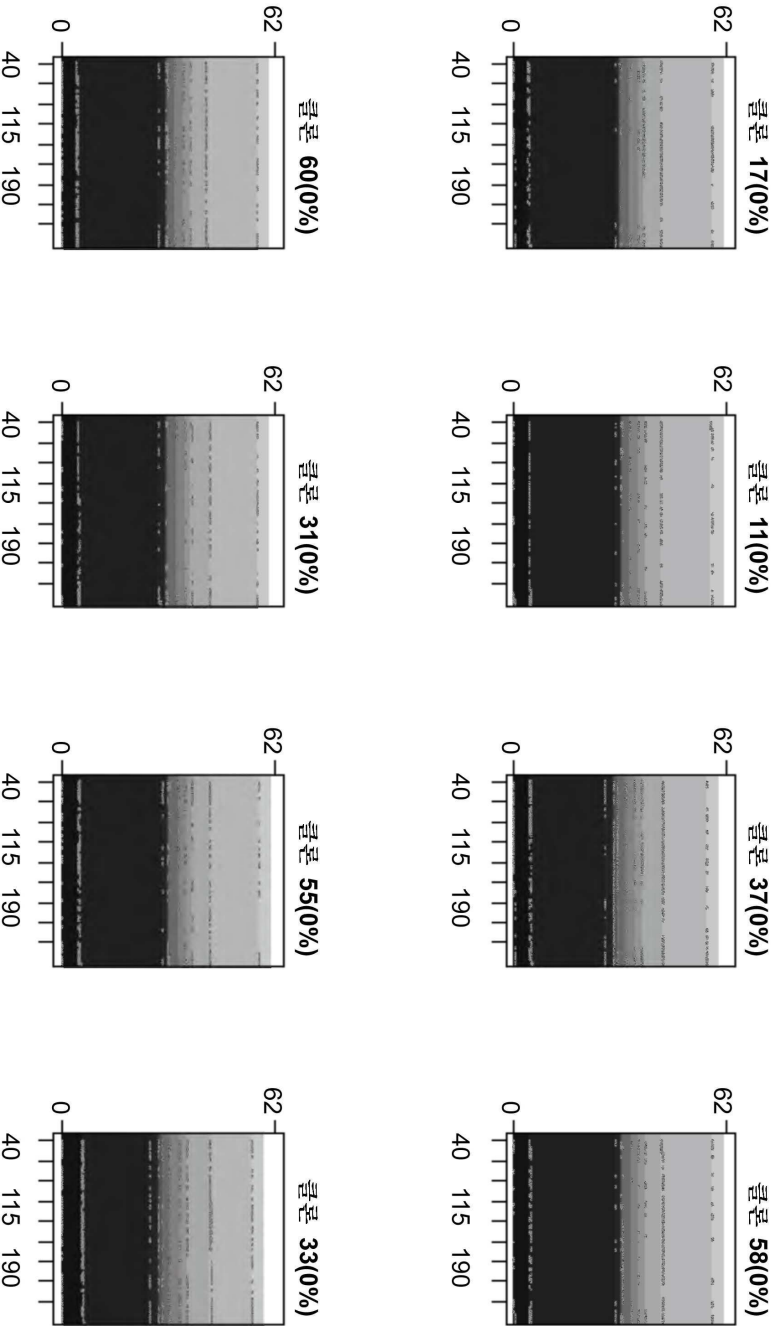
도면14ii

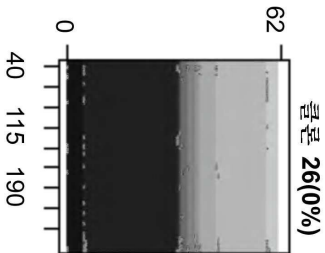
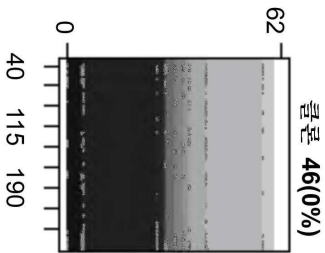
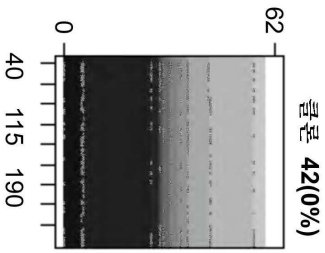
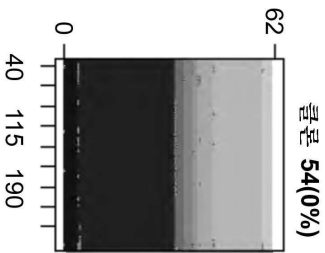
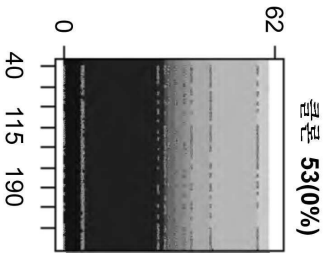
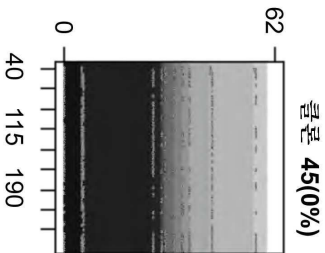




도면14iii

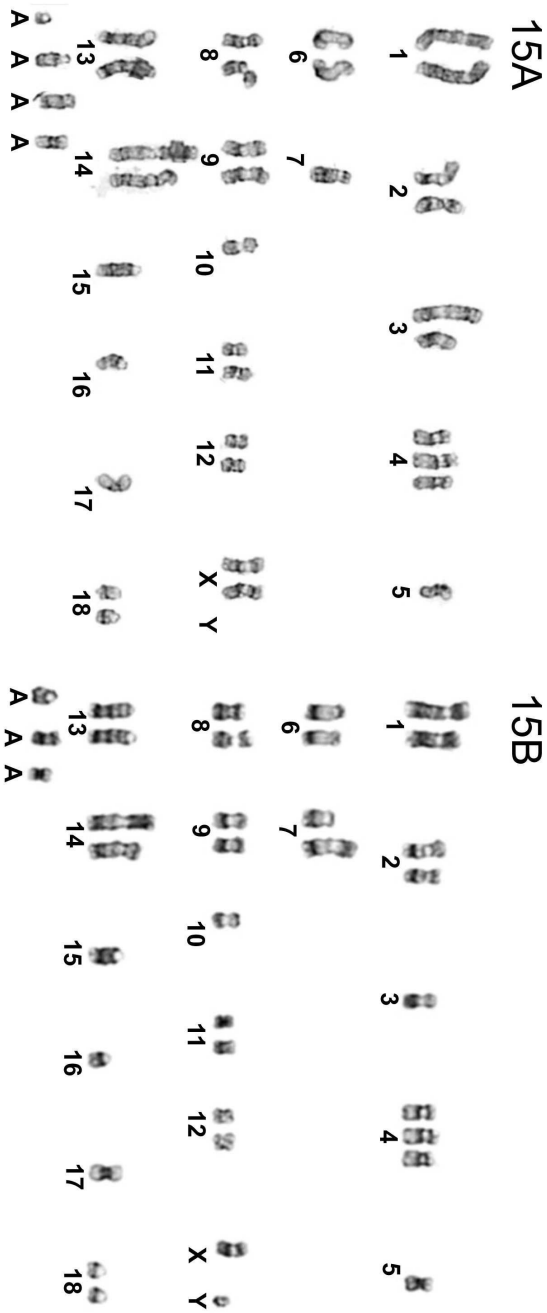
도면14iv





도면14v

도면15



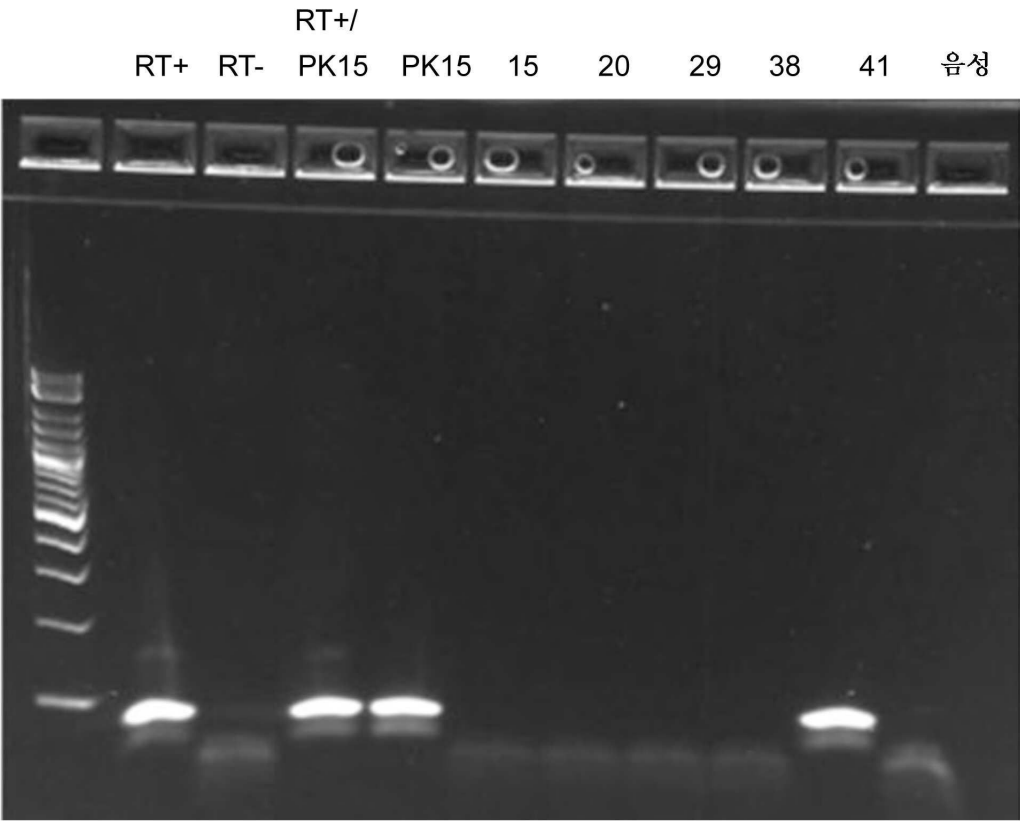
도면16

	PK15-1974	클론 15	클론 20	클론 29	클론 38	클론 40	클론 41
염색체 1							
염색체 2		add(2) (p14.2)		add(2) (p14.2)	add(2) (p14.2)		add(2) (p14.2)
염색체 3	add(3) p15	add(3) (p15)	add(3) (p15)	add(3) (p15)	add(3) (p15)	add(3) p15	add(3) (p15)
염색체 4		(+4)	(+4,+4)	add(4) (p13.1)	add(4) (p15.1), add(4) (p13.1)	(+4,+4,+4)	(+4)
염색체 5	-5	-5	-5	-5	-5	(-5,-5)	-5
염색체 6	-6						
염색체 7	-7	-7	der(7;16) (q10;q10)	-7	-7	der(7;16) (q10;q10)	-7
염색체 8							
염색체 9	-9						
염색체 10	-10	-10	-10	-10	-10	-10	-10
염색체 11	-11						
염색체 12							
염색체 13							
염색체 14	t	der(14;15) (q10;q10), add(14) (p10)	der(14;15) (q10;q10), add(14) (p10)	der(14;15) (q10;q10), add(14) (p10)	der(14;15) (q10;q10), add(14) (p10)	der(14;15) (q10;q10), add(14) (p10)	der(14;15) (q10;q10), add(14) (p10)
염색체 15							
염색체 16		-16		-16	-16	-16	-16
염색체 17	(-17)(17) (q10)	(-17)(17) (q10)	(-17)(17) (q10)	(-17)(17) (q10)	(-17)(17) (q10)	(-17)(17) (q10)	(-17)(17) (q10)
염색체 18							
X,Y	XX	XX	XX	XX	XX	XX	XX
A	n/a	+4mar [8]	+1~5mar [cp10]	+4mar [9]	+3~4mar [cp10]	+1~5mar [cp10]	+4mar [5]

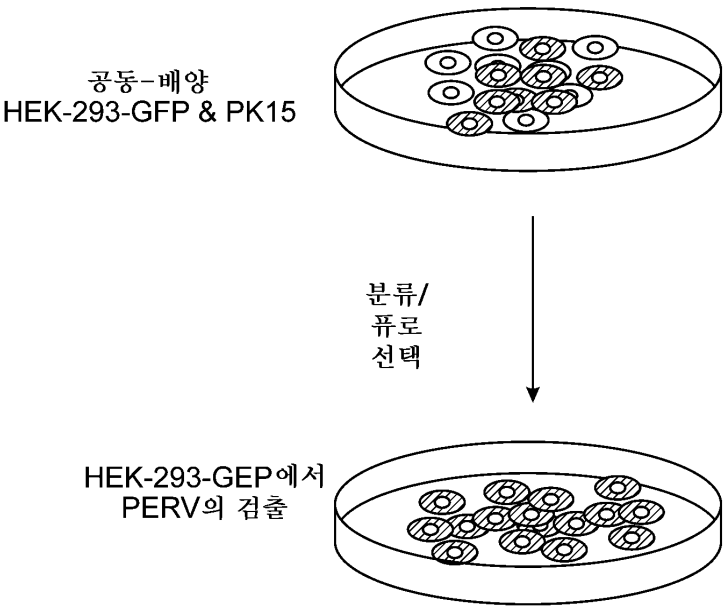
도면17

명명법	의미
+	염색체의 획득
-	염색체의 상실
(:)	파단 (상세한 설명에서)
()	주위 구조적으로 변경된 염색체 및 파단점
add	미지의 기원의 추가적인 물질
der	유도체 염색체
i	동위염색체
p	염색체의 짧은 아암
q	염색체의 긴 아암
t	전위
a	이상

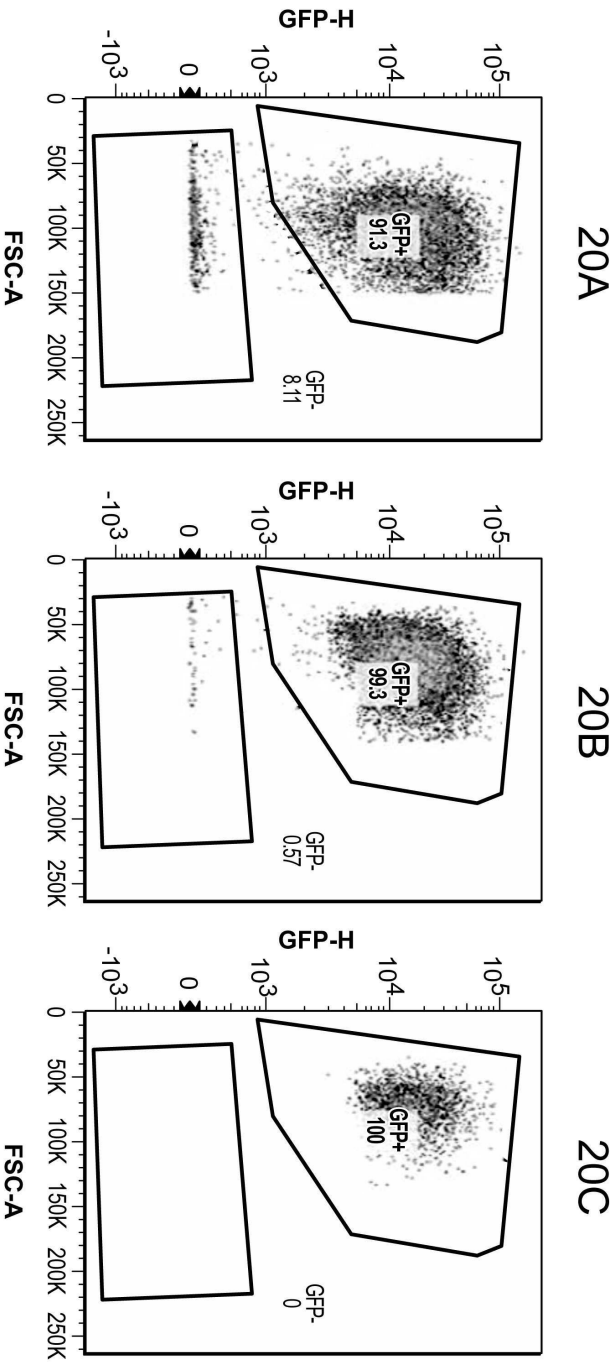
도면18



도면19

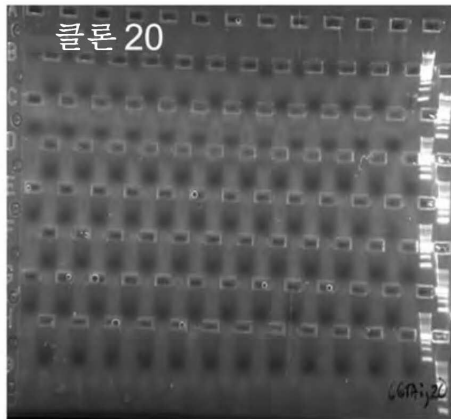


도면20

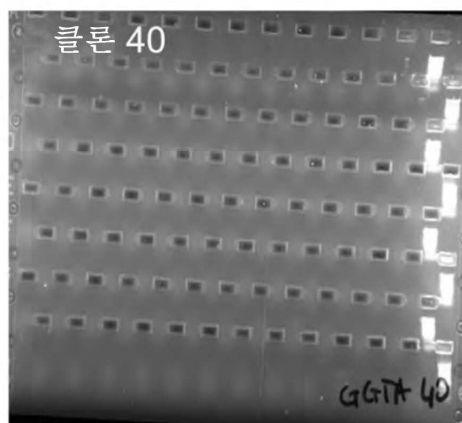
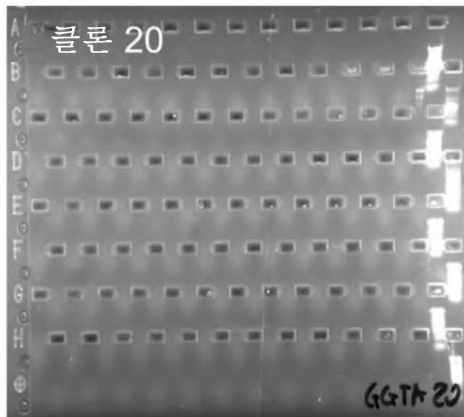
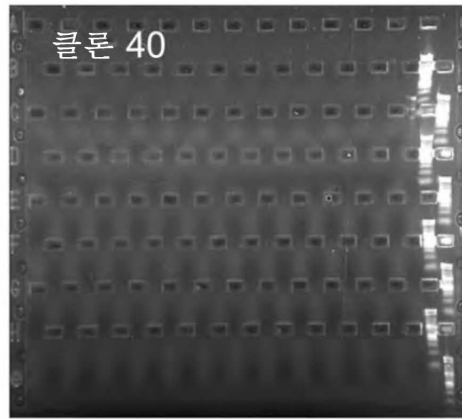


도면21

21A



21C

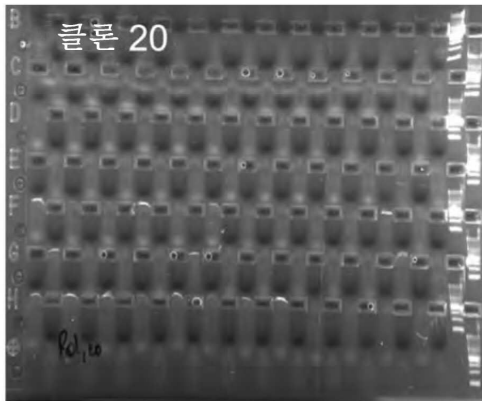


21B

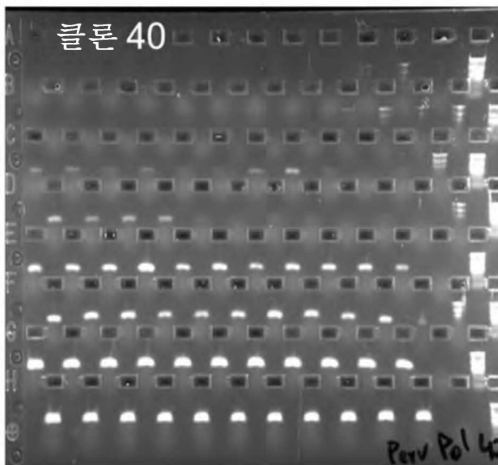
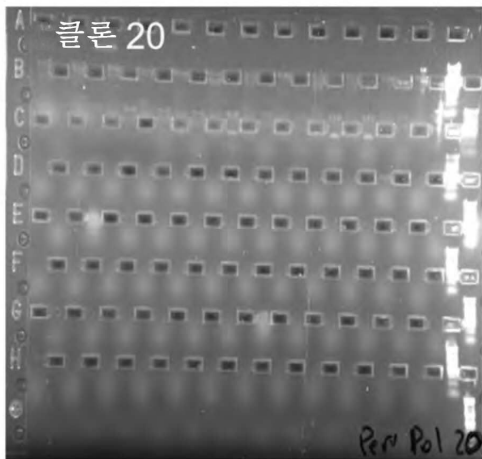
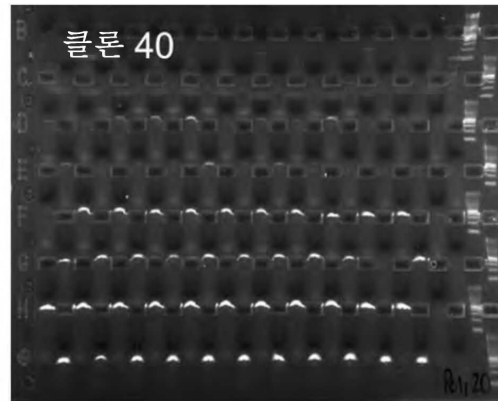
21D

도면22

22A



22C

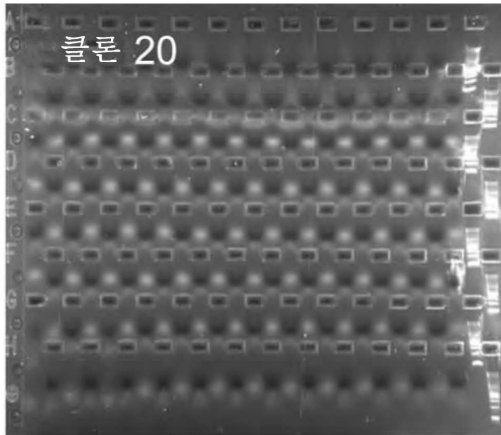


22B

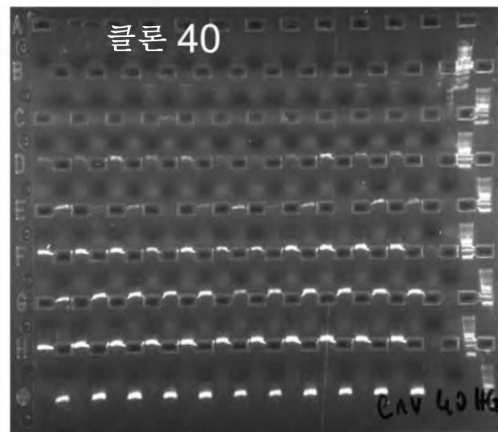
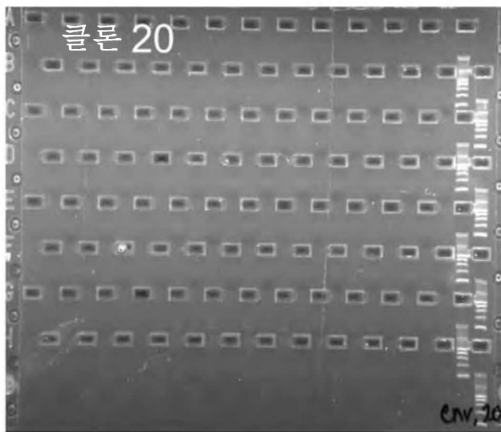
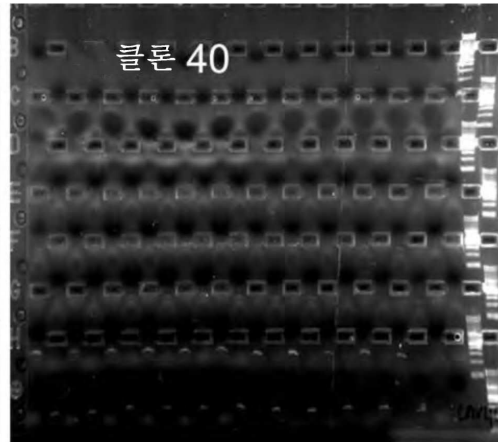
22D

도면23

23A



23C

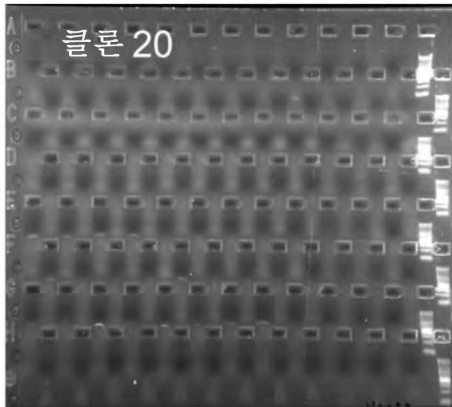


23B

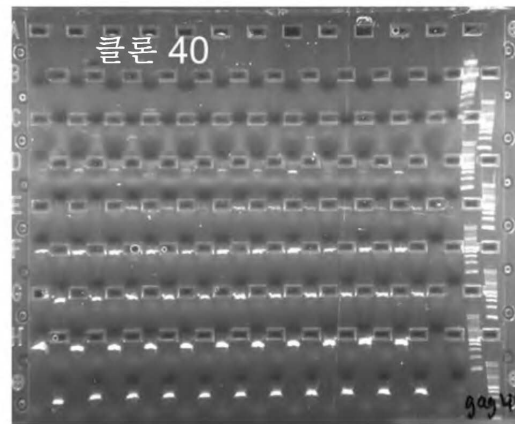
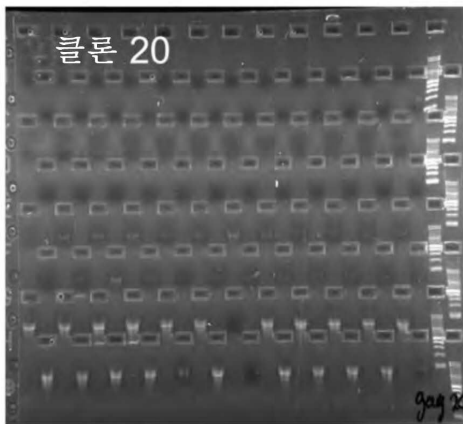
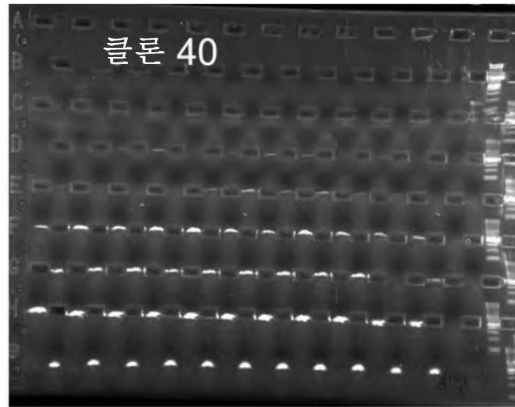
23D

도면24

24A



24C

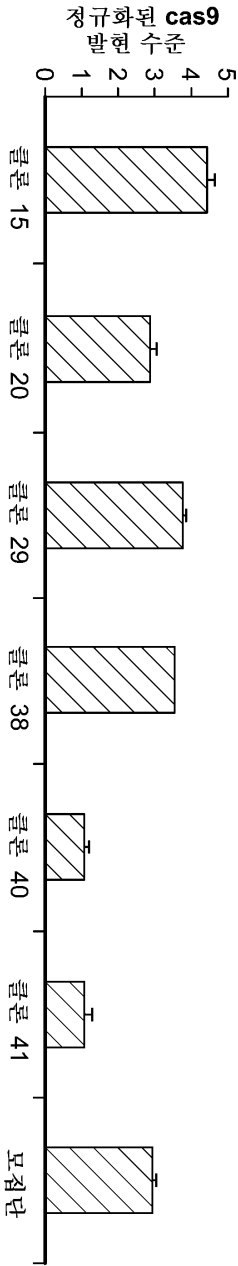


24B

24D

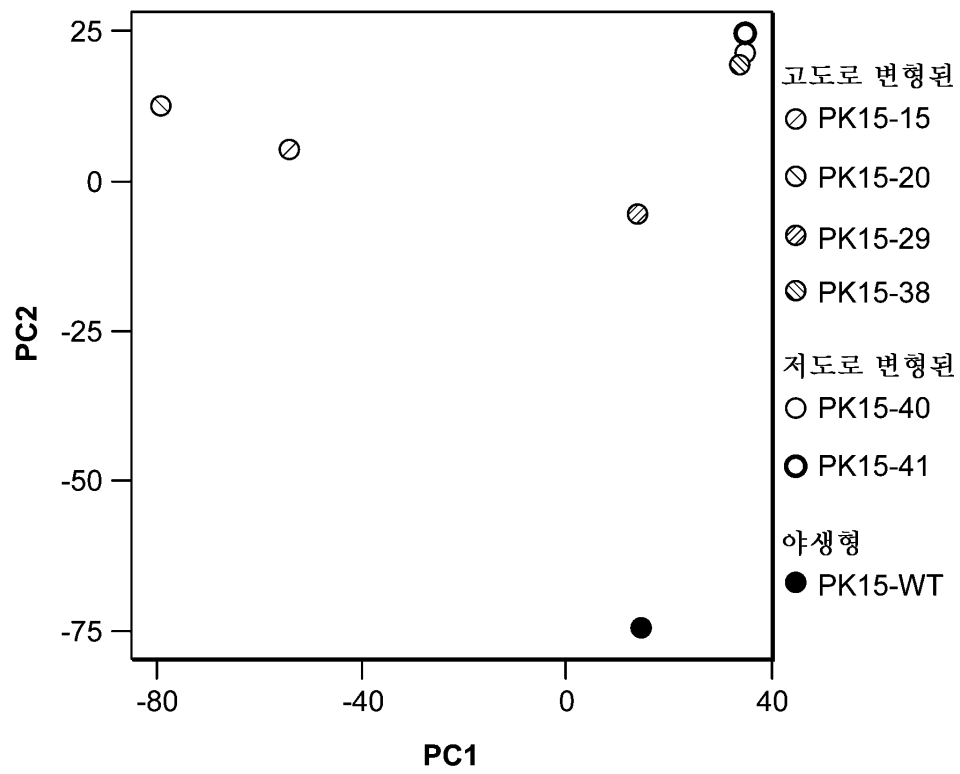
	클론 15	클론 20	클론 29	클론 38	클론 40	클론 41	PK15
Cas9	782	771	207	416	61	78	0
gRNA1	5	3	2	1	0	0	0
gRNA2	4	4	2	1	0	0	0
총	75815790	72609563	82295929	72569325	60990510	80508090	0

25A



25B

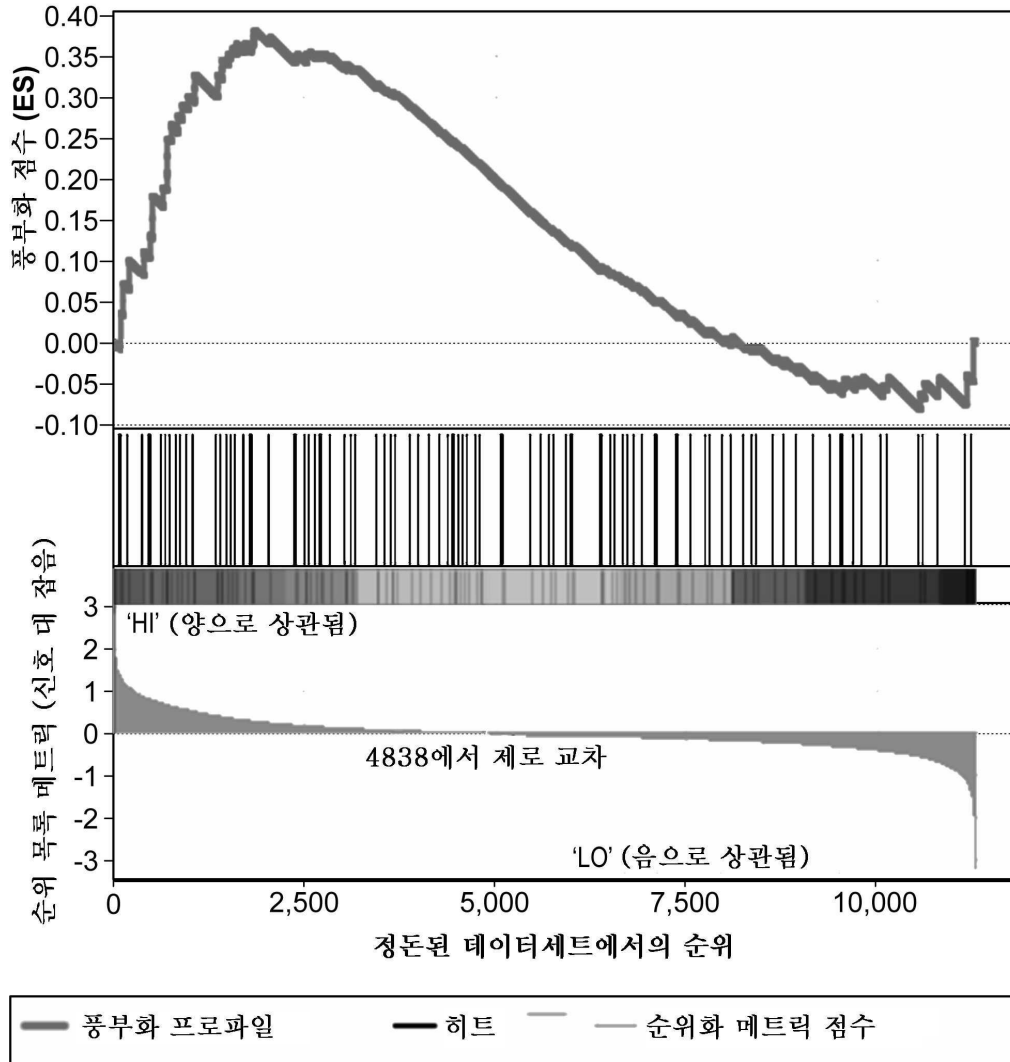
도면26



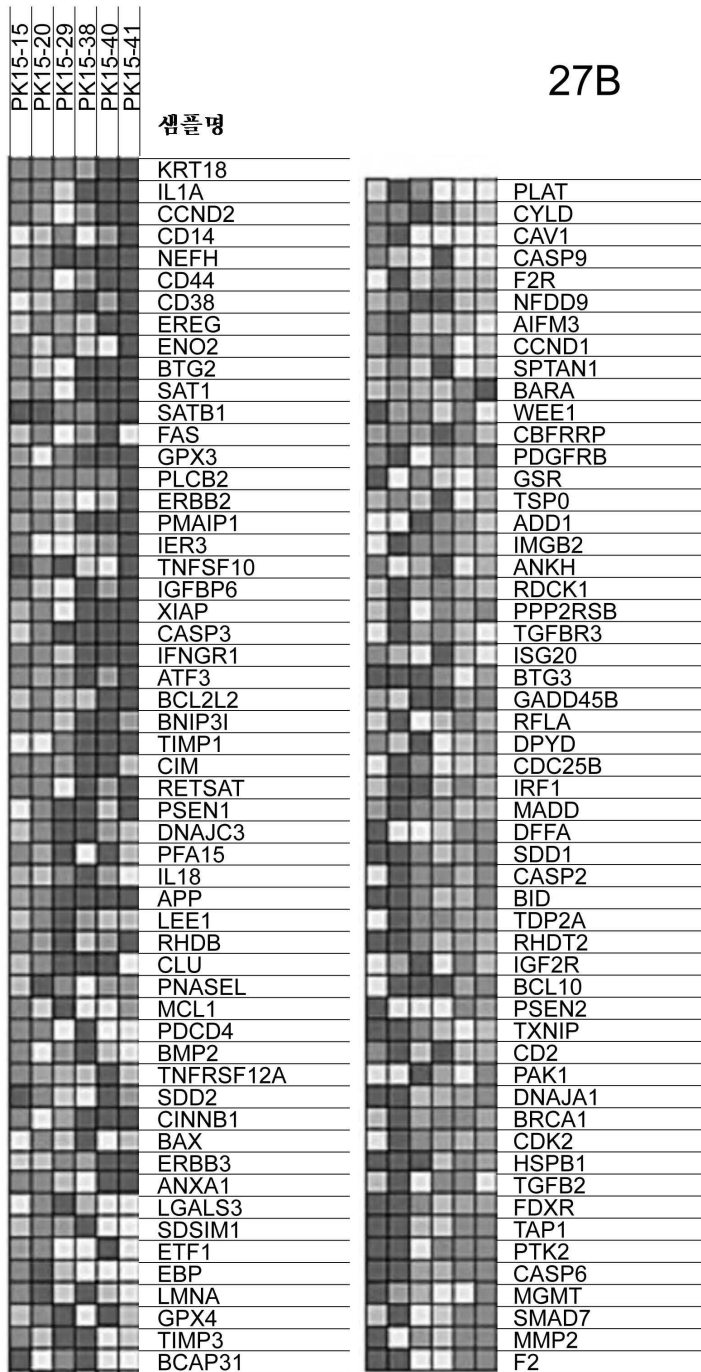
도면27i

27A

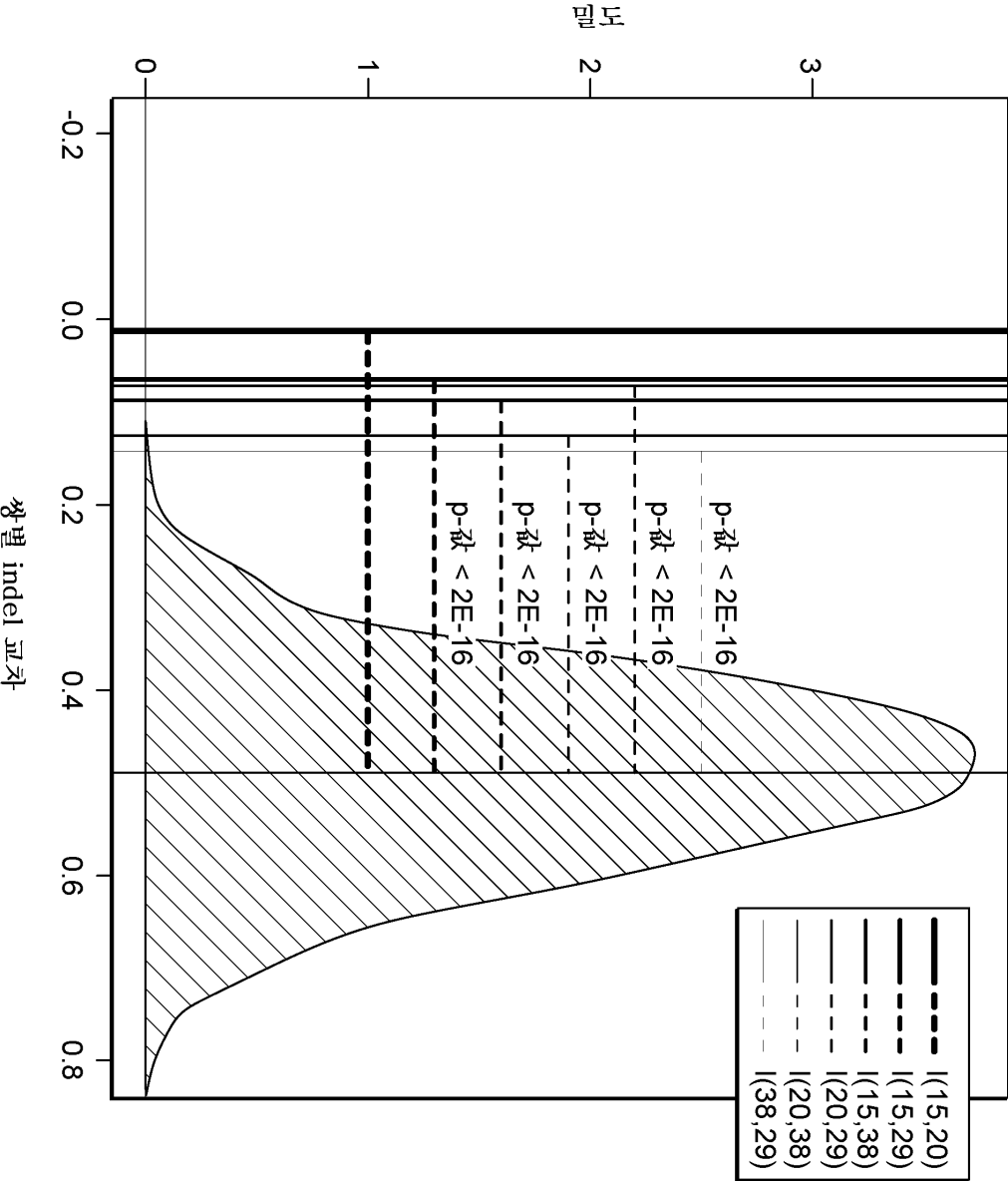
풍부화 플롯: 특징_아포토시스



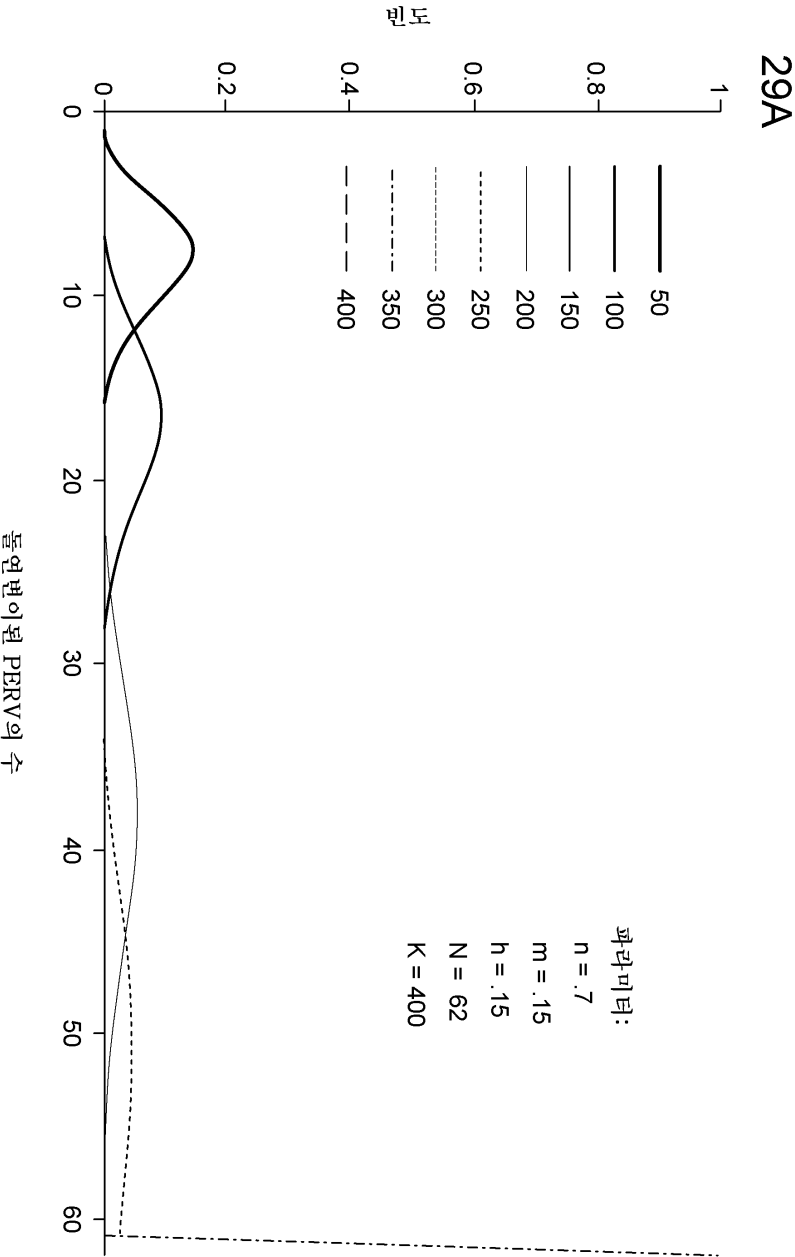
도면27ii



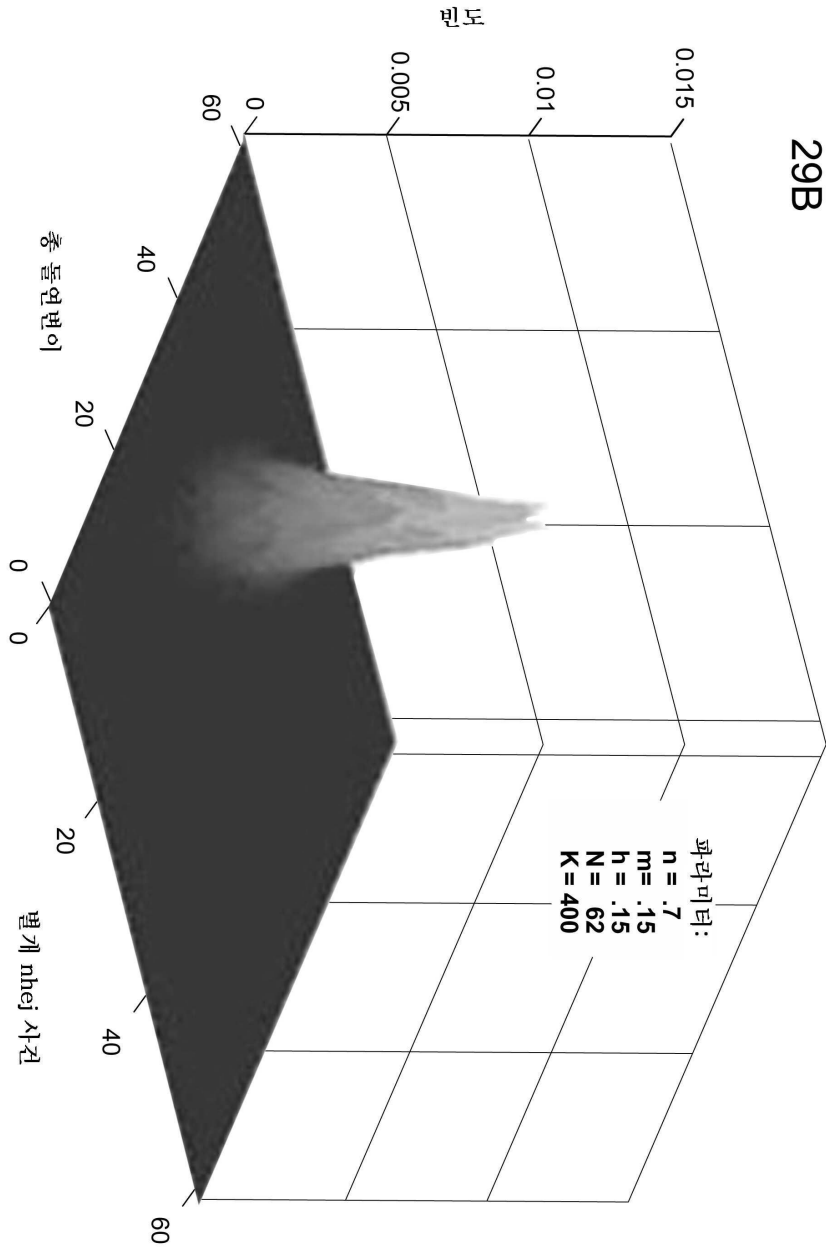
도면28



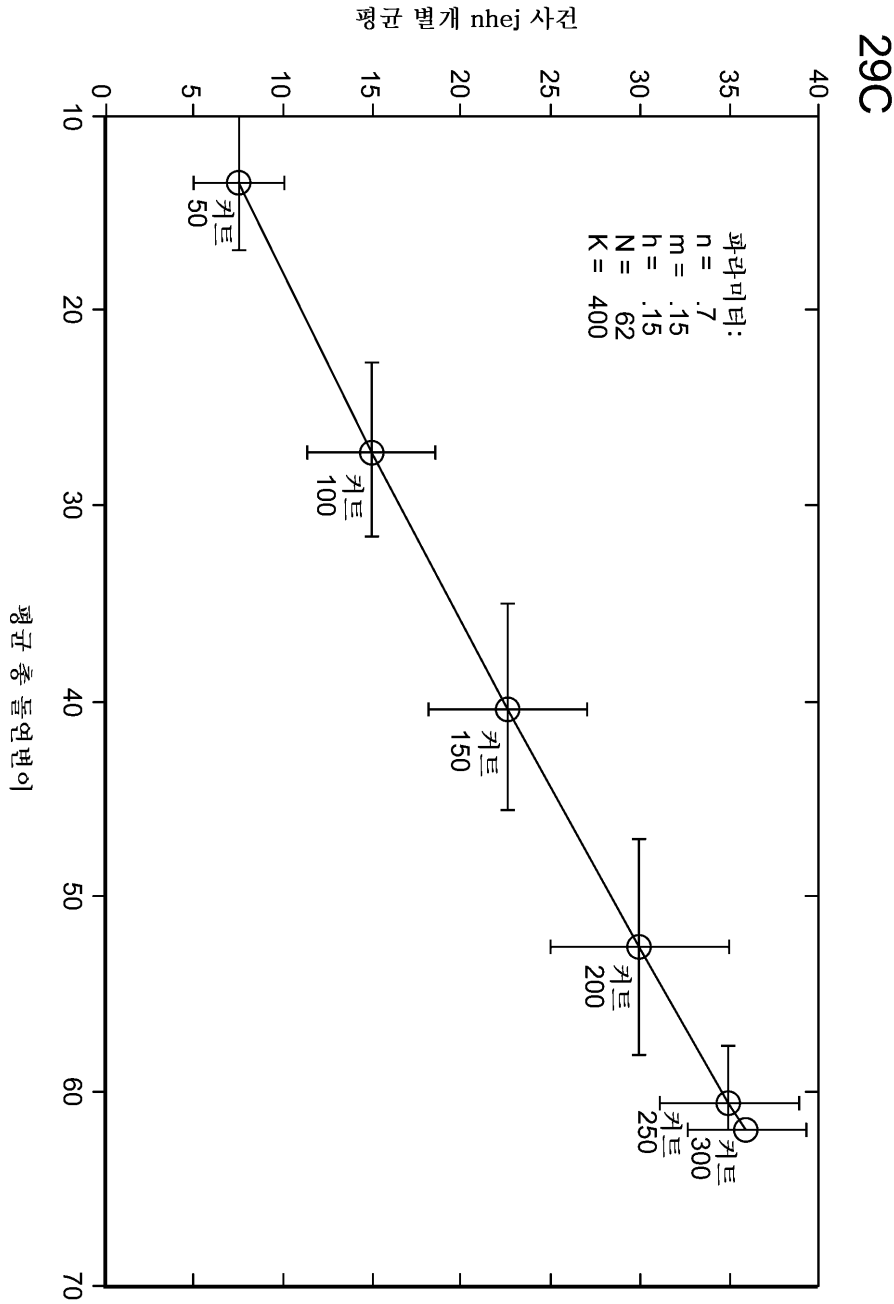
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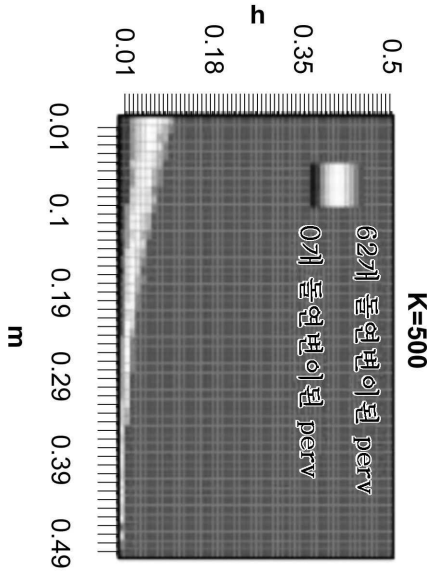
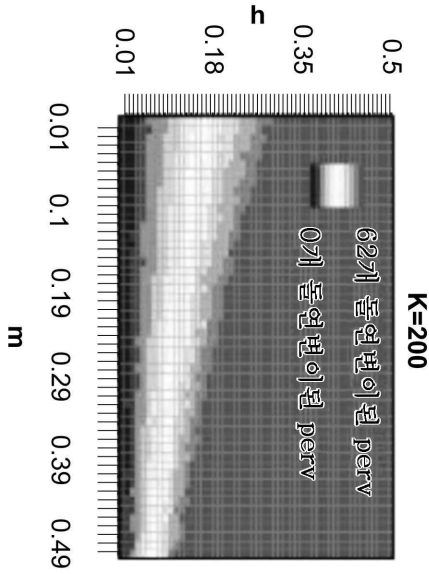
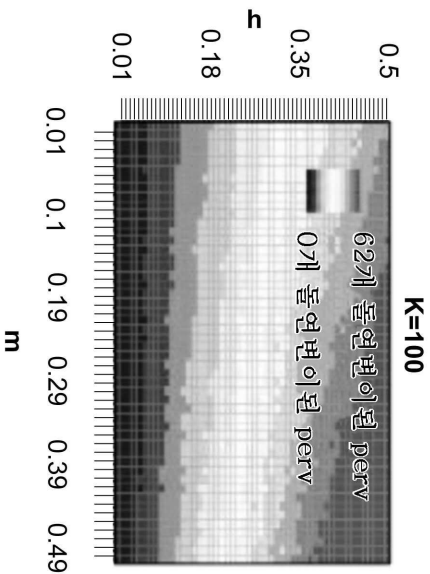
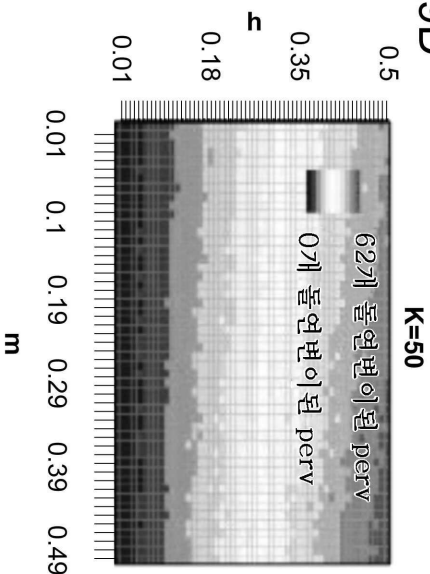
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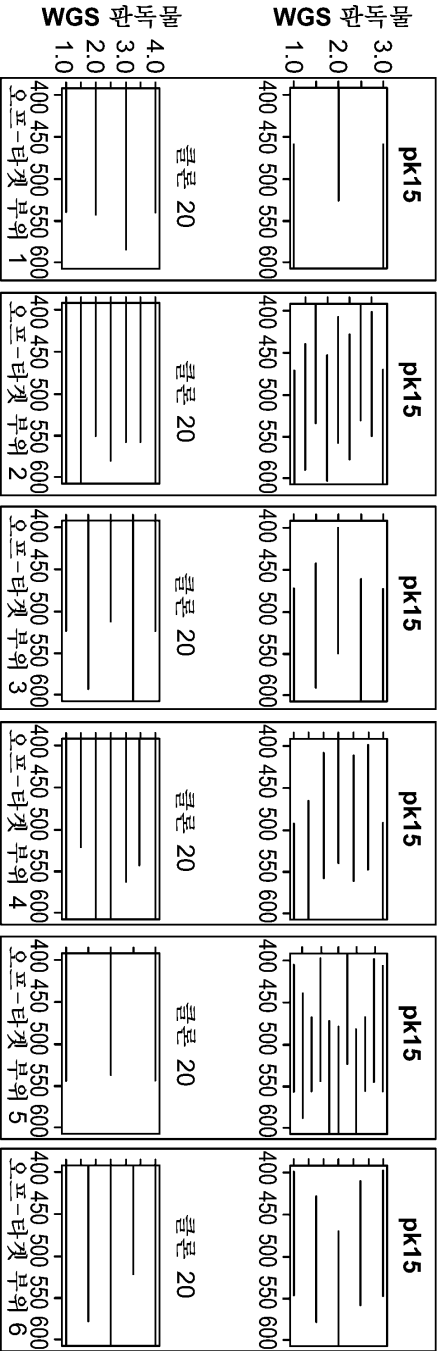


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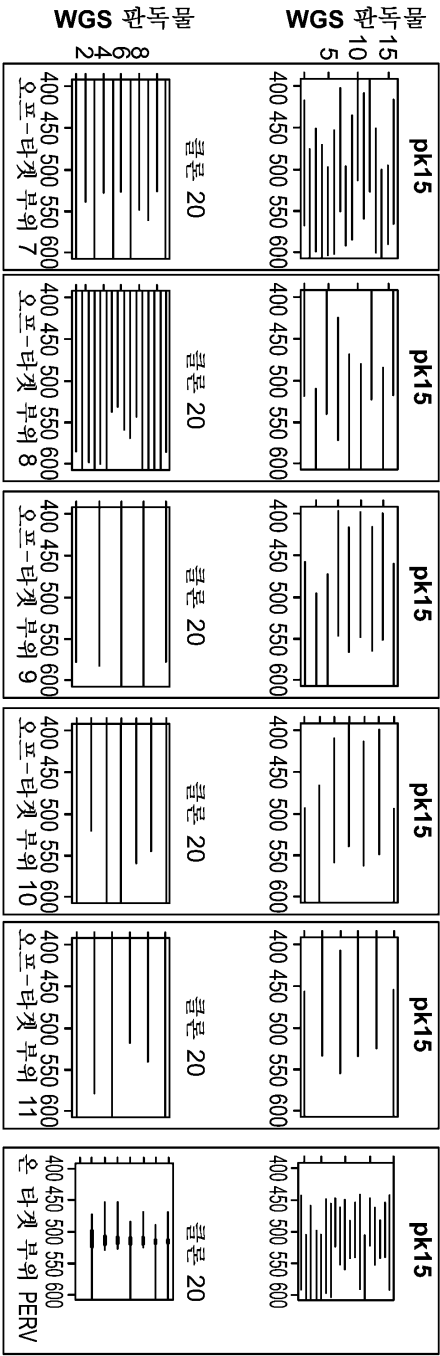


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