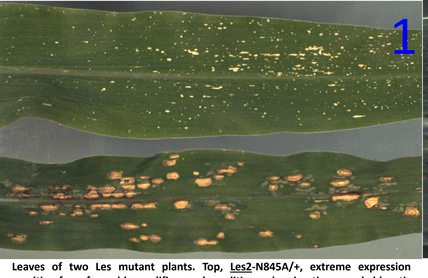
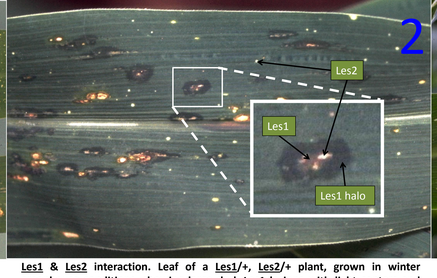


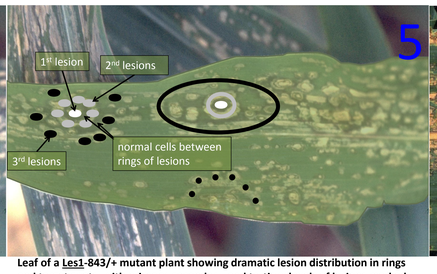
Leaves of two Les mutant plants. Top, Les2-N845A/+, extreme expression resulting from favorable modifiers and conditions, showing tiny round chlorotic dots becoming small white necrotic lesions. Bottom, Les1-N843/+, showing small greyish necrotic spots enlarging in concentric circles to become light brown necrotic lesions. Note that lesion pattern for a particular size appear as pieces of circles.
图一：两个Les突变体植株的叶片。图上：Les-2-N845A/+在适宜环境及修饰基因作用下的极端表现，显示小型圆的褪绿斑点逐渐变成小型白色坏死病斑。图下：Les1-N843/+，显示小型灰色坏死斑点呈圆形向外扩散变成淡褐色坏死病斑。注意特定大小病斑图案很像一个圆环。



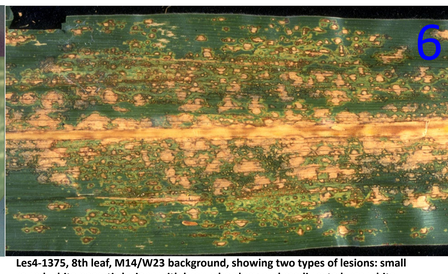
Les1 & Les2 interaction. Leaf of a Les1/+, Les2/+ plant, grown in winter greenhouse conditions, showing large dark Les1 lesions with light centers and dark watery halos and small round white necrotic Les2 lesions. Some Les 2 lesions appear within the halo of a Les1 lesion. The dark watery halos reflect the outward cell to cell movement of dying cell contents or a message that may cause adjoining healthy cells to become necrotic and die.
图二：Les1, Les2的交互作用，Les1/+, Les2/+生长在冬天温室条件下植株的叶片，显示大型淡色中心的黑色水轮状Les1病斑，以及小圆白色坏死Les2病斑。有些Les2病斑显然在Les1病斑水轮里面。黑色水轮代表死亡细胞内含物向外部细胞扩散或是传达一个信息，导致相邻细胞开始坏死或死亡。

Leaf of a homozygous csp1 (les*-NA1173) mutant plant showing many small white nearly transparent spots.
图五：纯合csp1 (les*-NA1173) 突变植株叶片，显示许多小型白色接近透明斑点。

Leaf of a Les1-843/+ mutant plant showing dramatic lesion distribution in rings and target spots, grown under unusual winter greenhouse conditions. Target spots reflect two types of signaling from dying cells: (1) direct cell to cell contact; and (2) across living cells to a new initiation site.
图三：突变体Les1-843/+，在不正常冬天温室条件下，植株叶片显示极端的圆形及目标点的病斑分布。目标点反映来自死亡细胞的两种类型信息。1）细胞与细胞的直接接触，及2）病斑细胞跳过生存细胞而产生新的诱发位置。



Leaf of a Les1-843/+ mutant plant showing dramatic lesion distribution in rings and target spots, with primary, secondary, and tertiary levels of lesions marked.
图四：突变体植株Les1-843/+显示极端的圆形及目标点的病斑分布，图中标示初级，次级及三级程度病斑。



Les4-1375, 8th leaf, M14/W23 background, showing two types of lesions: small round white necrotic lesions with brown borders; and medium to large white necrotic irregularly shaped lesions.
图六：遗传背景是 M14/W23的Les4-1375第八叶片，显示两种类型的病斑：小圆白色，褐色周边的坏死病斑；以及中型到大型白色不规则形状坏死病斑。

(see also mutants.maizegdb.org)

Lesion Mimics, Target Spot: Model for Cell Death Signalling

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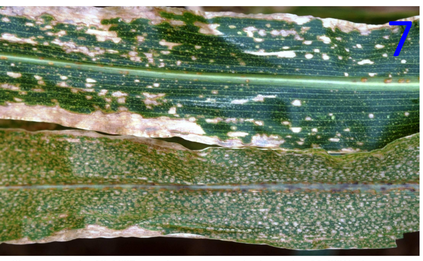
The disease lesion (*Les*) mimics are the most frequently occurring dominant mutants from EMS mutagenesis in maize. From the screening of over 50,000 M1 plants for all variations of the lesion phenotype, we have identified 51 separate dominant cases. A much smaller, though probably comparable number of recessive *les* mutants, have been seen but not considered in this report.

The mutants range widely in expression, but have the common phenotype of leaf lesions that are strikingly similar to those caused by various leaf blight diseases. In all cases tested, the phenotypes have occurred in the absence of a pathogen. They are initiated by sunlight and certain chemicals, and can be chlorotic, necrotic, or sequentially both. The lesions of different mutants vary in size, shape, color, frequency, distribution, time of onset, position, rate of expansion, sharpness of boundaries, *etc*. In some mutants, the lesions expand to cover the leaf, resulting in senescence. It appears that particular cells on the leaf surface are, at specific developmental stages and within certain specifically variable temperature ranges, highly susceptible to damage by sunlight.

We hypothesize that two signals are involved. The first arises from dissolution of the cell membrane, which releases highly active cell contents that cause lethal damage to neighboring cells. This damage spreads continuously outward, forming a necrotic lesion that stops growing when conditions change. The second signal is revealed by the "Target Spot" oscillatory phenotype; a central spot of dead tissue surrounded by alternating rings of healthy and dead tissue. This phenotype suggests signaling between dead and living cells, across living tissue, that causes lesion formation. This signal may proceed more rapidly than the first, through several ranks of normal cells without damaging them during a diurnal cycle of conditions that do not favor lesion formation.



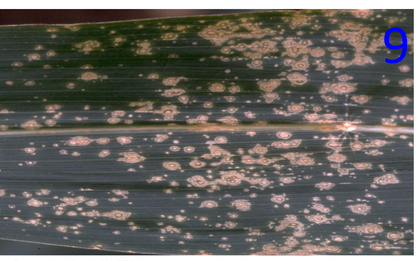
8th leaf of Les10-A607/+ heterozygous mutant plants. Mo20W (top) and M14/W23 (bottom) backgrounds, for comparison of respective genetic modifiers.
图七：遗传背景是 Mo20W （图上）及M14/W23（图下）的Les10-A607/+第八叶片，在不同遗传背景下性状表现比较。

8th leaf of Les3-A781 homozygous mutant plant showing various sizes of necrotic lesions (photo courtesy D. Hoisington).
图八：纯合 Les3-A781突变植株第八叶片，显示各种大小坏死病斑（戴夫，贺欣顿提供图片）。

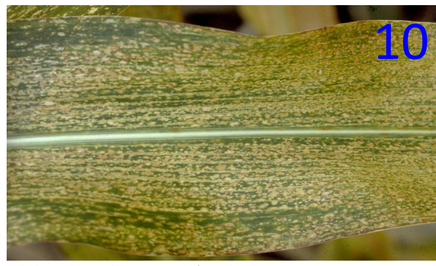
模拟病斑，目标点，细胞死亡信号模式

杰瑞，纽佛1；张铭堂1：多尼，卡兹克2；久哈，戈木克3
1密苏里大学植物科学部，2 密苏里大学，信息学院，电脑学系及植物小组
3 普渡大学生物及植物病理系

玉米使用EMS诱变剂所产生的显性突变体，模拟病斑的突变是最常见的一类。对超过50,000 M1植株进行所有类型病斑表现型筛选，我们鉴定出51个独立显性病斑表现型事件。我们也观察到一些隐性。非常小型的病斑。这些病斑不在本文考虑中。



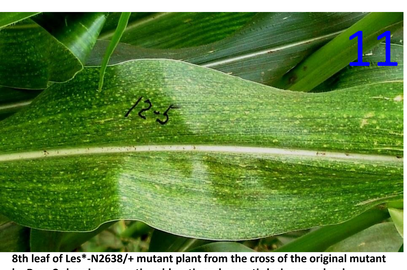
8th leaf of Les*-N1378/+ plant, showing tiny to medium-sized necrotic lesions with white center and brown and tan concentric rings.
图九：Les*-N1378/+突变植株第八叶片，显示细小到中型，中心白色，外面环绕褐色及黑褐色环状坏死病斑。



Section of the eighth leaf of a Les11/+ plant showing many small chlorotic and necrotic lesions.
图十：Les11/+植株第八叶片部分，显示许多小型褪绿及致死病斑。

突变体之间，表现型差异巨大，但是叶片病斑的情况与由病菌侵袭叶片所产生的病害斑点，具有非常类似而一致的表现型。所有这些突变斑点的表现型，都是在没有病害侵入的情况下产生。阳光及某些化合物可能是诱发病斑原因，可能是不能合成足量叶绿素，或局部叶片组织坏死，或二者同时发生。不同突变体坏疽斑点的大小，形状，颜色，频率，分布，发生时间，位置，扩张速率，以及边缘明确的程度等，各不相同。某些突变体病斑扩展覆盖整个叶片，导致叶片早衰死亡。似乎叶片表面某些特定细胞在特定发育时期及某一特定温度变异范围，对阳光特别敏感而容易受到损害。

我们假设病斑形成包括两个信号。第一是由于细胞膜溶解，释放大量高活性细胞液，导致邻近细胞致死的损害。这个损害持续向外扩张，形成坏死病斑，直到环境条件改变而停止扩张。第二个信号显示的是目标点重复性表现型。就是一个中心组织死亡点，被一圈活组织，一圈死亡组织，重复交替环绕。这种表现型建议，信号可以透过生命组织，决定组织生存或死亡，导致病斑交替发生。这种信号的传递比第一种更快，可以透过多层活细胞而不损害它们。可能是由于两种不同生育条件交替改变，在不适合病斑形成的条件下，形成一圈一圈没有遭受损害的活组织。



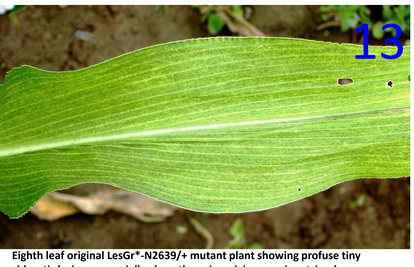
8th leaf of Les*-N2638/+ mutant plant from the cross of the original mutant by Rscm2 showing many tiny chlorotic and necrotic lesions randomly scattered along leaf blade.
图十一：使用最初突变体与Rscm2材料杂交的Les*-N2638/+突变植株第八叶片，显示许多小型褪绿及坏死病斑，沿着叶片逢机散布。

Eighth leaf of Les*-N2590/+ mutant plant from outcross on Mo20w showing moderate size rectangular shaped chlorotic to white necrotic lesions distributed in an unique pattern, namely clustering in groups that appear to be the remnant of a target spot pattern at more than one level. Note that some of the larger lesions take a "C" form.
图十二：遗传背景是 Mo20W杂交的Les＊-N2590/+第八叶片，显示中度大小四角型褪绿到白色坏死病斑的特殊分布形式 。就是一群围绕目标中心四周密集而形成的好几层残余病斑。注意，某些较大病斑呈C型。

I. Target Spot mechanics (Images 2-4)
- A. Lesion initiation requires dominant allele of Les1
  1. Sunlight
  2. Temperature below 72° F
  3. Particular developmental stage
- B. Two signal types
  1. Cell to cell movement of dying cell fluids
  2. Unknown signal travels through normal cells without affecting them, until initiation conditions occur.

II. Variant Les expression, different genes (Images 5-13)
Genetic modifiers Mo20w vs. W23 (Image 7)

III. In other species
- A. Maize Les22 encodes UROD (Image 14)
- B. Humans Cutaneous Porphyria (Image 15)
- C. Ring of brown aging skin spots (Image 16)



Eighth leaf original LesGr*-N2639/+ mutant plant showing profuse tiny chlorotic lesions, especially along the veins, giving a grainy striped appearance.
图十三：原始的LesGr*-N2639/+突变体植株第八叶片，显示扩散性小型褪绿病斑，特别是沿着叶脉，显示颗粒状条型外观。

Les Mutant Phenotypes

Les mutants: total of 51 dominant mutants from approximately 50,000 M1's screened. One possible allelic pair among 22 tested leads to an estimated 200+ loci. These are likely to be important in disease resistance.

Phenotypic variables to consider:

-size, shape, color, texture, and lesion profile.

-frequency, timing, distribution, and developmental patterns.

-response to genetic and environment modification

-relationship to actual disease symptoms and resistance

Attention is drawn to possible developmental relationships that are exhibited by certain patterns of lesions and the implication of signaling between cell groups and in other species.

- Porphyria in humans and Les22; both encode UROD

- Cell death signaling in mice

List of Images

1. Les2 and Les1 different lesion types
2. Heterozygous Les1 and Les2: comparison of lesion types
3. cps1 clear spots
4-5. Les1 target spots, two types of signals
6. Les4 late expression
7. Les10 Mo20w vs. W23 modifiers
8. Les3 progressive lesion enlargement
9. Les*-N1378 two types of lesions
10. Les11 prolific small lesions
11. Les*-N2638 many tiny chlorotic lesions
12. Les*-N2590 different type of target spot
13. Les*-N2539 tiny chlorotic (grainy) lesions
14. Les22 Phytoporphyria encodes UROD (maize)
15. Cutaneous Porphyria encodes UROD (human)
16. Ring brown aging skin spots (human)
(UROD = uroporphyrinogen decarboxylase)

Leaf of a Les22 mutant plant showing phytoporphyria symptoms (lesions) in maize; encodes uroporphyrinogen decarboxylase (UROD). 图十四：玉米突变体Les22植株叶片显示的植物血色素症状（病斑）； 这个基因控制产生血色素合成脱碳氧化酶或UROD。

Cutaneous porphyria; mutant gene encodes uroporphyrinogen decarboxylase (UROD).
图十五：吸血鬼症； 基因控制产生血色素合成脱碳氧化酶或UROD，这个酶控制血液合成第三 步骤。突变基因不能合成。以致在晒太阳后，形成紫色血斑。

Ring of brown aging skin spots on human forehead.
图十六：老年人前额皮肤形成的老化褐色圆斑。