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Preservation of Coast Redwood on Alluvial Flats

Because man has altered the environment, active management is now required.

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Twice during the last 9 years, the North Coast region of California has suffered major flood damage. During December 1955 and January 1956 and again during December 1964, logs, lumber, and even sawmills were swept down the Eel, Van Duzen, and Klamath rivers. Farms were washed away or buried under thick layers of mud and debris, transportation and communications were disrupted, and several small communities were completely leveled.

This destruction was widely reported; less well publicized was the havoc these floods caused in the old-growth coast redwood [*Sequoia sempervirens* (D. Don) Endl.] groves that dominate the alluvial flats along the Eel River. Trees were uprooted and carried downstream, and the herbaceous cover within the groves was buried beneath as much as 120 centimeters of stream-carried silt. The alluvial flats of Rockefeller Forest of the Humboldt Redwoods State Park along Bull Creek, a tributary of the Eel River, were particularly hard hit. During a 2-week period in December 1955 and January 1956, Bull Creek turned into a raging torrent, uprooted more than 300 redwoods greater than 120 cm in diameter at breast height, and literally carried away the 20 hectares of alluvial flats on which they had grown (*1*). The loss did not stop there. Subsequent erosion of the weakened stream banks has destroyed an additional 224 large trees and 6 more hectares of alluvial flats (*1*). In view of the fact that prior to 1955 there were only 200 hectares of redwood-stocked alluvial flats in the entire Rockefeller Forest, the loss of 26 hectares is of great importance. Similar patterns of destruction were evident on the alluvial flats all along the Eel River.

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Future floods must be checked if recurring major economic losses are to be prevented and if the alluvial-flat redwoods are to be preserved for the enjoyment of future generations. Strong regulatory control by the state, possibly with public acquisition, of critical watersheds along with manipulation of stream channels and vegetation have been suggested as a possible solution; but such a program would never completely control erosion, flooding, and silting. Furthermore, even if such a program should be approved in its entirety, its impact could not be fully realized for many years to come. An alternate suggestion—the construction of a system of flood control and water storage dams—could, if carried out, control peak stream runoff and thus directly reduce flood damage. Because strong public support for this last approach has developed, it is probably the plan that will be adopted.

Any enthusiastic support for a program of dam construction, however, must be tempered with the realization that although a series of dams will solve one problem, their presence will create new, and perhaps even more complex, problems for those trying to preserve alluvial-flat redwoods. With the elimination of intermittent flooding and silting, the environment within which the magnificent alluvial-flat redwoods have developed will be drastically altered. The flats will be invaded by plants previously unable to compete with redwood because of the unique physiological capacity of the latter to withstand inundation and siltation. These invaders will have to be controlled (*2*). In addition, the mineral cycling of nitrogen, phosphorus, and the other elements required for growth will be altered, and over the years it may even be necessary to apply fertilizer to maintain the health of these redwoods.

Here we describe the environment under which the alluvial-flat redwoods have developed, the physiological characteristics that have allowed redwood to exploit this environment, and the impact that flood control will have on the alluvial-flat redwoods unless it is counterbalanced by techniques to preserve vegetation.

The Environment

After the December 1964 flood, personnel of the Humboldt Redwood State Park discovered the exposed ends of three logs protruding from the bank along a small stream which flows into Bull Creek. These logs were buried 9, 16, and 26 meters beneath a deposit of sand, coarse gravel, and boulders (Fig. 1). Curious as to what kind of trees they were and how old they might be, the park superintendent had sections cut from the end of each protruding log and sent them to us for identification and dating. The presence of

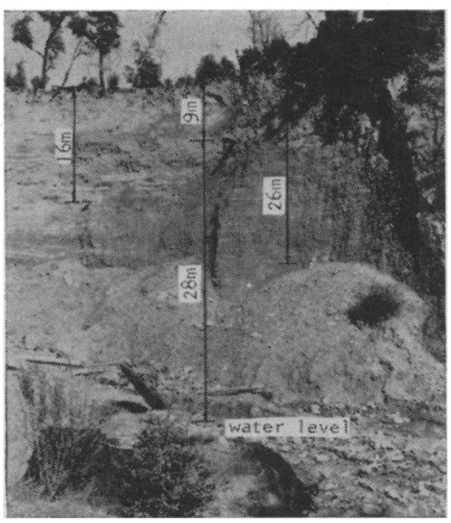

Fig. 1. Exposed ends of three Douglas fir logs (9500 ± 120 years old) in a stream-cut bank on Cuneo Creek, a tributary of Bull Creek, Humboldt, California. [Courtesy of H. King]

thick-walled epithelial cells and longitudinal tracheid cell walls with prominent spiral thickenings established the wood as Douglas fir [*Pseudotsuqa menziesii* (Mirb.) Franco] (*3*).

Heartwood samples from each section were carbon-dated. The ages of the trunks buried at 9, 16, and 26 meters were found to be 9540 ± 120, 9500 ± 120, and 9450 ± 120 years old, respectively (*4*). The striking similarity in ages suggests that a great deal of material was deposited relatively rapidly some 9500 radiocarbon years ago.

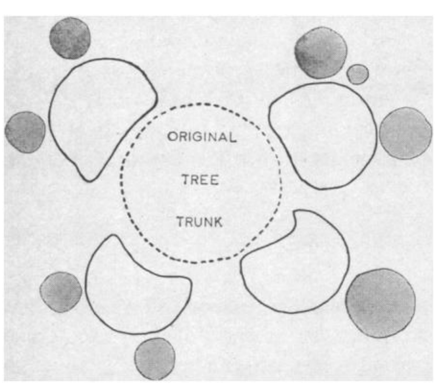

Fig. 2. Schematic representation of the development of a fairy ring (shaded trunks). Repeated fires for more than several hundred years critically injured the tree in the center. In response to this injury, it sprouted from its base. Of these sprouts only three or four survived. The others, along with the critically injured mother tree, were killed and consumed by successive fires. As this sequence is repeated, the ring enlarges until it finally loses its identity among the surrounding trees.

An examination of the site at which the logs were discovered indicated that the material in which they were buried was water-borne because a distinct bedding pattern was evident. The nearly parallel orientation of the trunks further supports this interpretation. The lack of any obvious discontinuities in the bedding and the similarity in ages of the three logs buried at quite different depths suggest a steady, rapid rate of deposition.

The logs and the sediments in which they were buried probably did not come from the watershed of the small side stream, which is less than 260 hectares in area and is insufficient in size to account for the depth of the deposit. The material was probably laid down by Bull Creek itself at a time when it occupied a different channel.

Heavy erosion upstream and subsequent deposition downstream have continued to play a dominant role in the Bull Creek drainage. Zinke (*5*), working on an exposed stream-bank face along Bull Creek within the Rockefeller Forest, has shown that 15 major floods in the past 1000 years have caused the deposition of sufficient silt (each forming a distinct profile) to raise the elevation of these alluvial flats more than 9 meters. Thus, it appears that periodic and occasionally severe erosion in the upper reaches of the Bull Creek drainage, followed by flooding and silt deposition along the alluvial flats downstream, have been a prominent and continuing feature of the natural environment and are part of a pattern going back at least 9500 years.

Fire has also been a part of the redwood's environment. This is evidenced by the presence of fire scars, the stratification of charcoal throughout the alluvial deposits, and the development of fairy rings (Fig. 2).

Physiological Characteristics of Redwood

Because of certain physiological characteristics, redwood has been able to occupy and dominate alluvial flats along the Eel River, not in spite of, but along with flooding and fire. One of these characteristics is apparently negative geotropic root growth in which roots can and do grow upward into flood-deposited silt from roots buried beneath it. We first attempted to study this phenomenon by artificially creating

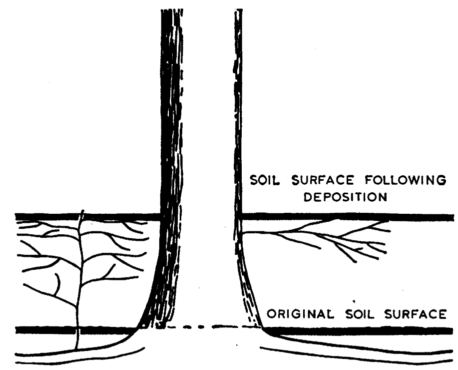

Fig. 3. Schematic representation of the development of a new root system after the burial of the old root system beneath flood-carried silt. Initially, new roots grow vertically upward from the buried roots (left). Later, after several years, a new horizontal root system develops adventitiously from the buried trunk (right).

a silted environment by piling silt and gravel to various depths around the bases of a number of large trees in the Rockefeller Forest. This operation proved to be too costly, so we adopted an alternate plan which, although not a duplication of silting, created a root-free zone overlying an extensive, and only partially damaged, root system. We removed soil to a depth of 60 centimeters and for a radial distance of 12 meters from around each of four trees with a bulldozer and then immediately pushed it back into place. Over 90 percent of the small feeder roots were destroyed, but the horizontally oriented anchor roots were left essentially intact.

By 1960 (1 year after bulldozing), new roots arising from the underlying root system were found to have grown vertically upward through this root-free soil layer (*6*). So strong was the stimulus for this upward growth that many root tips literally grew out of the ground and could be found protruding up to several millimeters above the soil surface.

However, this system of root regeneration (Fig. 3) is, in itself, inadequate to account for the continued survival of redwood subjected to repeated silting. If such a system alone were operating, the bole and root system of the tree would, after a number of silt layers had been laid down, take on an umbrella shape, with the trunk forming the shaft and the vertically oriented root system forming the ribs. This form does not develop. Instead, evidence from a number of toppled trees reveals that a second root system develops adventitiously from the buried portion of the stem and that eventually these roots form an entirely new root system. The old root system with its vertical extensions then dies. In this way, the functioning root system moves successively higher up the stem of the tree (*7*) as flood-deposited silt continues to build up around its base (Fig. 4).

Redwood produces seed fairly regularly over most of its entire range (*8*). Along the alluvial flats in the Eel River drainage, it is sufficient to bring about a spring blanket of seedlings wherever mineral soil is exposed. Few, if any, of these seedlings survive through the first season, however, unless the forest canopy is open enough for sunlight to reach the forest floor. Shortly after germination, root elongation becomes dependent on photosynthesis. Where photosynthesis is restricted, root elongation quickly falls behind in its race with depletion of soil moisture, and sometime during the rainless summer the seedling succumbs to insufficient moisture—provided, of course, that a rodent or a hungry slug has not already done away with it. The role of mineral soil in seedling survival is an indirect one. Its exposure merely guarantees that certain root-attacking fungi residing in the organic mantle of the soil have been removed. Sterilization with the organic mantle still intact apparently achieves the same result (*9*).

Redwood reproduces vegetatively from adventitious buds concentrated just above the root crown. Most of the adventitious buds are held in check by a regular flow of growth substance down the stem. Interruption of this flow by an injury to the stem or crown permits the buds to break, and sprouts follow. These buds are evident on 1-year-old seedlings, but additional ones form as the tree develops. However, attrition is high, and, as the tree grows, many of the buds are killed. After several hundred years of growth, relatively few buds have kept abreast of diameter growth (Fig. 5). Through this process many of the older trees on the alluvial flats have already lost their sprouting capability.

Mature redwood is relatively resistant to fire. The stem is encased in thick bark which protects the tissue beneath and, if the crown should be killed, a new one can quickly regenerate from adventitious buds along the

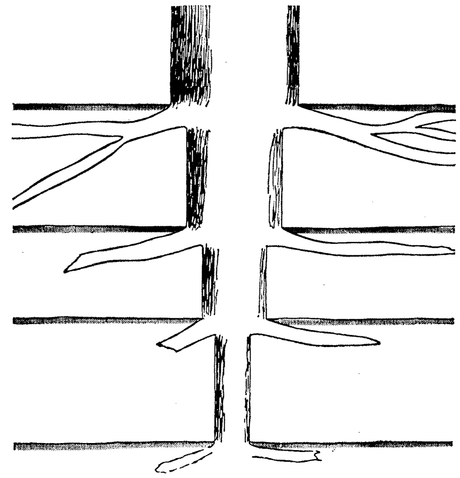

Fig. 4. Schematic representation of a tree that has survived three major root burials. After each burial, there was first a vertical invasion by roots from below and then eventually an adventitious root system originating from the trunk. Once established, this root system replaced the vertically oriented one which died.

stem and branches. The thick bark can be breached, however, by prolonged hot fires which then leave their scars in the wood beneath. These scars, in themselves, are not critical but serve as points of entry for heart rots and subsequent fires which over a succession of years can burn out the heart of a tree, leaving only a shell highly susceptible to windthrow.

Redwood does not have any insect enemies of consequence, and, once a tree becomes established, the only pathogens of significance are the heart rots. They are not killers, however, and they only weaken the tree indirectly by destroying the heartwood and making it more susceptible to windthrow.

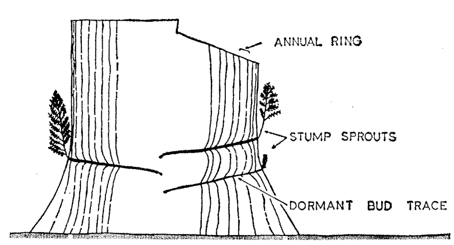

Fig. 5. Redwood reproduces vegetatively by sprouts that arise from dormant and adventitious buds concentrated just above the root crown. Large numbers of these buds can be found on small seedlings, but, as the tree becomes older, many are killed. Some, however, continue to grow outward with the tree and are suppressed in part by growth substances produced in the crown of the tree. Interruption of the supply of growth substance permits the buds to break and send up shoots.

Death comes to the alluvial-flat redwood as a result of raging floods, windthrow after fire damage, and heart rot, or a failure of the tree to maintain its balance. Considering the height and weight of these tremendous trees—many over 90 meters tall and weighing in excess of 100,000 kilograms—it is amazing that they can stand at all on the difficult footing that is afforded them by their alluvial-flat environment.

The key to their success lies in their ability to compensate for lean. The root platform resting on an unstable footing need sink only a bit under its load of 100,000 kilograms to cause the tree to tilt—a phenomenon not unlike that which caused the famous tower at Pisa to lean. But, unlike the Leaning Tower of Pisa, the lean of the redwood causes intensification of wood production on the underside which forms a supporting buttress and strengthens at the same time those roots that have been put under increased mechanical tension. It is not uncommon for all the trees on an alluvial flat to display some degree of buttressing, and occasionally the buttress may be several times wider than the diameter of the tree at right angles to it. Such trees are referred to locally as flatiron trees. The world-famous one in the Rockefeller Forest on Bull Creek is approximately 90 meters tall, 5.3 meters in diameter in the direction of the lean, and 1.4 meters in diameter perpendicular to the lean.

The ability to correct for lean and to stay erect depends on the rate at which the lean develops and the rate at which the tree produces wood. If the lean develops gradually on a healthy tree, wood production can usually keep pace with the lean. If the lean develops rapidly or if the tree is unhealthy at the start and produces only a limited amount of wood, the tree can soon become seriously unbalanced. Occasionally, such trees crash to the ground unexpectedly on a calm day for "no apparent reason." Usually, the unbalanced condition of these trees goes unnoticed until it is put to the test by heavy winds.

Only Douglas fir, tan oak (*Lithocarpus densiflorus* Rehd.), grand fir (*Abies grandis* Lindl), and bay (*Umbellularia californica* Nutt.) are potential competitors of redwood on alluvial flats in the Eel River drainage. These species are abundant on the surrounding slopes and intermittently deposit large amounts of seed onto the alluvial flats. Seed of all four species germinate readily on either mineral soil or on soil with a well-developed organic layer.

Initial seedling survival among these potential competitors, as with redwood, is generally best on exposed mineral soil. Whether this is due to rapid desiccation of the organic layer when present or to a root-attacking fungus has not yet been determined. Survival through the first year is dependent on photosynthesis, as it is in redwood. The net result is strong competition for space where breaks in the redwood canopy allow direct sunlight to reach the forest floor for at least some part of the day.

Fire kills seedlings and young trees of Douglas fir, grand fir, and bay, but not tan oak, which sprouts vigorously after fire. Flooding, if accompanied by heavy silting, kills seedlings, young trees, and even old trees of Douglas fir, grand fir, and tan oak. Thus, two of the species that are potential competitors of redwood on the alluvial flats are killed either by fire or flooding, one is killed only by fire, and one is killed only by flooding. Unlike redwood, none of these four potential competitors can withstand a combination of fire and flooding.

Preservation Management

Prior to the floods of 1955–56 and 1964, young growth of Douglas fir, tan oak, bay, and, to a lesser extent, grand fir were common on the redwood-dominated alluvial flats throughout the Eel River drainage because fire had been excluded as an environmental factor in the early 1930's. After these floods, three of these competitors were eliminated from the flooded portions of these flats. Only bay survived.

Once the Eel River is dammed, the second of the two environmental forces that have held the redwood's competitors in check over the last 10,000 years or more will be removed. Eventually, not only bay but tan oak, Douglas fir, and grand fir will partially or entirely replace redwood on the alluvial flats unless one or more interruptive factors can be introduced into the ecosystem to substitute for fire and floods.

It is too early to estimate the time required for redwood's competitors to complete this take-over. It will largely depend upon how long redwood can maintain its vitality in a fire-free, flood-free environment. The big "if" in this process is the impact of protection on the mineral cycle (Fig. 6). The extent to which mineral cycling has been modified by the exclusion of fire and the extent to which it will be further modified when flooding is eliminated are not known. The only study dealing directly with mineral cycling involving redwood suggests that blockage in the nitrogen cycle occurs, on some soils at least, under undisturbed conditions, that is, after the exclusion of fire (*11*). It has also been reported that changes in the microflora that bring about a major reduction in nitrate nitrogen production (*12*) occur in the absence of disturbance.

The role in the mineral cycle of the soil profile that is buried by silt during floods remains to be examined. Does it ameliorate cycle blockage, does it reinforce it, or does it have an impact all its own?

Blockage of the nitrogen cycle could bring about a rapid reduction in redwood vigor. If this occurs to any extent and if nothing is done about it, we can certainly expect the alluvial-flat redwood stands to disintegrate over the next hundred years or so.

Paradoxically, the fact that redwood is a long-lived species could be an important factor leading to its destruction under a program of protection, that is, protection from fire and floods. The vigor of a 1000-year-old redwood is difficult to assess, and even its death which may ensue as a direct result of such protection may take tens or even hundreds of years. The alluvial-flat redwoods could be dying before those responsible for their preservation become aware of it. Even now, the visitor who stops to admire and marvel at these giants may unknowingly be witnessing their losing struggle with death, not their preservation.

Unquestionably, preservation will require man's interference. Nevertheless, a number of conservationists with whom we have discussed this need for interference have been hesitant about assigning any active role to man. We frequently hear the complaint: "Why can't we leave it alone?" Herbicides, the ax, and the chain saw—all obvious tools to control the competing species —are almost always summarily rejected. Fire, on the other hand, is generally accepted in principle, but the involvement of men with rakes is highly upsetting. Time is running out for the alluvial-flat redwoods because of man's interference. It is too late to achieve preservation without man's counterinterference. Managed manipulation is the only solution to this preservation problem.

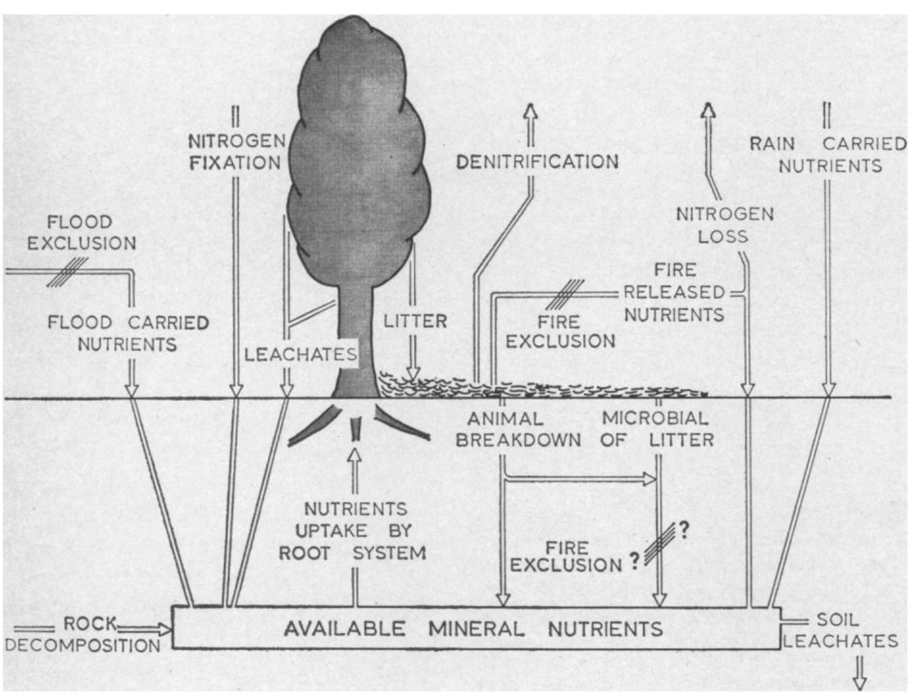

Fig. 6. Schematic representation of mineral cycling in a stand of mature alluvial-flat redwoods and the blockage (denoted by cross-hatching) that occurs after the exclusion of flood and fire.

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Paramutation: Directed Genetic Change

Paramutation occurs in somatic cells and heritably alters the functional state of a locus.

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It was observed about 10 years ago that an R^r gene in maize, which conditions anthocyanin formation in seed and plant, invariably has lowered anthocyanin-forming potential following passage through a heterozygote with the stippled (R^{st}) allele. The changed form of R^r was gametically transmissible. It reverted toward the standard type when made homozygous, but only partially. This unusual kind of heritable change was termed paramutation. The R^r allele in question was said to be paramutable, and the stippled factor was described as paramutagenic (*1*).

The initial studies revealed that paramutation involved chromosome components that do not conform to the ordinary rules of gene stability and integrity in heterozygotes. Furthermore, the induced heritable changes were directed. *R* paramutation appeared to be comparable in these respects to certain phenomena reported much earlier in *Pisum* by Bateson and Pellew (*2*), in *Malva* by Lilienfeld (*3*), and in *Oenothera* by Renner (*4*) as anomalous exceptions to Mendelian inheritance. The *R* case in maize offered advantages for experimental analysis which these other systems lacked, and it has been intensively investigated. The present article is limited to discussion of the *R* studies, for the most part, but the results appear to be meaningful for paramutation in general.

The biological significance of paramutation rests on the fact that the phenomenon involves constraint on gene expression during development of the individual which is exerted by factors located within the chromosome itself. The illuminating advances made in recent decades in characterizing the genetic substance biochemically have disclosed genomic components in bacteria that function *in situ* to regulate the action of genes specifying protein structure (*5*). The chromosomes of higher organisms are vastly larger and more complex than their counterparts in bacteria, and one may expect to find that they too embody devices whereby gene action is regulated locally. Paramutation is of general interest for the clues it may give to the nature of gene-controlling mechanisms.

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Induction of Paramutation

The general problem which paramutation presents is illustrated by the results of a simple experiment. Pollen of three kinds of maize plants, with a common highly inbred background, is applied to the silks of $r^g r^g$ individuals as follows:

1) $r^g r^g$ ♀ $\times R^r R^r$ ♂
2) $r^g r^g$ ♀ $\times R^{st} R^{st}$ ♂
3) $r^g r^g$ ♀ $\times F_1 R^r R^{st}$ ♂

R alleles condition anthocyanin formation in the plant and in the aleurone—the outer cell layer of the endosperm. The recessive r^g allele conditions development of colorless aleurone and colorless plant (lacking in anthocyanin). R^r, termed "standard R^r," represents a class of factors, of wide geographic distribution, that conditions pigment formation in both aleurone and plant. The endosperm is the product of a fertilization separate from that which gives rise to the accompanying embryo. It receives a double complement of genes from the female parent, and one set from the male parent, and so is a triploid structure. Standard R^r in single dose ($R^r\, r\, r$) gives darkly mottled aleurone, and in either two doses ($R^r R^r r$) or three doses ($R^r R^r R^r$), gives self-colored aleurone. R^{st} (stippled) gives a spotting pattern in the aleurone, directly proportional to dosage.

The endosperm genotypes which result from the above three testcrosses are

1) All $R^r r^g r^g$
2) All $R^{st} r^g r^g$
3) 50 percent $R^r r^g r^g$ plus 50 percent $R^{st} r^g r^g$

Half of the seeds ($R^r r^g r^g$) resulting from mating 3 should conform genetically to those from mating 1, and the other half should conform to the seed resulting from mating 2. The latter