spectively. A narrow-sense heritability of 0.13 was determined from cone yields in 16-year-old progeny.

The broad-sense heritabilities indicated moderate genetic control of fruitfulness. The narrow-sense heritability indicated a low additive genetic component. An appreciable amount of nonadditive genetic variance was suggested by the large difference between the narrow-sense heritability and the broad-sense heritabilities and by the variation in flower and cone production.

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Effects of Clone and Light Intensity on Photosynthesis, Respiration and Growth of Aspen-Poplar Hybrids[1]

By G. E. GATHERUM, J. C. GORDON, and B. F. S. BROERMAN[2]

(Received for publication July 1, 1966)

Introduction

A naturally-occurring aspen-poplar hybrid *(Populus grandidentata* X *P. alba)* shows promise as a timber tree in southeastern Iowa. It has the superior form and growth habit of bigtooth aspen and the rapid growth rate of white poplar. Mean annual growth rate of the hybrid is 3% times greater than the growth rate of native oaks on the same site at age 24 (MCCOMB and HANSEN 1954). To date, four clones have been identified, the Shimek and Sherrill in Van Buren County, and the Crandon and Hansen in Lee County. The Shimek and Sherrill clones have been described in detail by LITTLE *et al.* (1957). To maintain the existing but unknown superior genotype, stem cuttings have been used exclusively for planting material. However, survival and growth of outplanted cuttings of the Shimek and Sherrill clones have been low. LITTLE information is available concerning survival and growth of the Crandon and Hansen clones. Therefore, fundamental investigations of physiological variation among the four clones have been initiated to determine the causes of poor survival and growth and to determine variation in gene-controlled production.

To determine physiological variation among the four clones, rates of physiological processes were measured under controlled environmental conditions. Because of their importance as yield determining processes, photosynthesis and respiration were chosen as dependent variables for the initial investigation of among-clone physiological variation. Because light intensity strongly affects rates of photosynthesis, and thus may affect survival and growth, rates of photosynthesis and respiration were determined at several light intensities. To test the feasibility of using such physiological data in the development of rapid selection methods, the relationship must be known between rates of physiological processes and growth and distribution of assimilate. Therefore, growth and distribution of assimilate also were determined for the four clones.

Thus, the dependent variables included in this study were (1) rates of photosynthesis (2) rates of respiration (3) growth and (4) distribution of assimilate. The independent variables were (1) clone and (2) light intensity. The hypotheses tested were:

1. Differences in photosynthesis and respiration of aspen-poplar hybrids exist among clones and light intensities.
2. Differences in growth and distribution of assimilate of aspen-poplar hybrids exist among clones.

An excellent summary of the research on the effect of environmental factors on tree photosynthesis and respiration was written by KRAMER (1957). Studies showing differences in photosynthesis, respiration and/or growth among seed sources or clones of trees include investigations by HUBER and Polster (1955), RÜSCH (1959), HUBER and RÜSCH (1961), MCGREGOR *et al.* (1961), KRUEGER and FERRELL (1962), POLSTER and WEISSE (1962), BOURDEAU (1963), GATHERUM (1965), and others.

Materials and Methods

Photosynthesis and respiration of aspen-poplar hybrids were determined (1) at light intensities of 560, 1,300, 2,008, 3,300 and 6,000 foot-candles and (2) for four clones, Hansen, Sherrill, Crandon and Shimek, obtained originally from naturally-occurring stands in southeast Iowa. The study was established as a simple split-plot experiment with four replicates of five light intensity plots, each divided into four clone sub-plots. Photosynthesis and respiration of intact potted plants were measured in a gas-tight, refrigerated, controlled-environment chamber described by BROERMAN *et al.* (1966). A Beckman L/B infra-red analyzer, model 15 A, was used to measure the uptake and evolution of CO, within the chamber. In addition, growth and distribution of assimilate of aspen-poplar hybrids were determined for each of the four clones. This study was established as a randomized complete block design with 20 replicates of four-clone plots.

Stem cuttings of the four clones were obtained from a clonal orchard in December, 1963. The cuttings were (1) graded by diameter, .60 of an inch, and length, 9 inches, to minimize variation related to cutting size, (2) placed in polyethylene bags and treated with a fungicide and (3) stored in a refrigerated seed house at 38^0 F until May 8, 1964. At this time, the cuttings were butt-end treated with 100 ppm-concentration of indole-butyric acid for 24 hours and potted in 1-gallon pots in a soil mixture of one-third sand, one-third peat and one-third Clarion loam. The potted plants were grown in the State Forest Nursery at Ames

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[1] Journal Paper No. J-5379 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1582.

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under full sunlight and at moisture levels close to field capacity. Measurements of photosynthesis and respiration were begun on June 10, 1964 and ended on June 23, 1964. Potted plants were taken to the laboratory; soil moisture was brought to field capacity; and the pot was placed in a 3-mil polyethylene bag which was tied at the base of the plant to prevent evolution of CO_2 from the pot soil to the chamber. The potted plant was sealed in the chamber at a constant temperature of 15 ± 0.2^0 C and preconditioned at the desired light intensity for 15 minutes. At the end of the preconditioning period, uptake of CO_2 by the plant (net photosynthesis) was measured for a 5-minute period followed by a 5-minute measurement of evolution of CO_2 by the seedling in the dark (dark respiration). The plant was placed in the dark by turning off the lights and placing black photographic cloth around the chamber. Gross photosynthesis subsequently was estimated by adding net photosynthesis and dark respiration. The plant was removed from the chamber, and the following measurements were recorded: shoot length; fresh and dry weight of top, leaf, stem and root; and leaf area. Each leaf was traced on paper immediately after determination of photosynthesis and respiration, and leaf area was determined later by planimeter. Dry weight measurements were recorded after the leaves, stems and roots were dried for 24 hours at 70^0 C.

Analyses of variance and covariance were made and simple correlations computed at the Iowa State University Computation Center. Differences among clone means were tested for significance with DUNCAN's multiple range test (DUNCAN 1955), and differences among the unequally-spaced light intensity means were tested with a modification of orthogonal regression comparisons (STEEL and TORRIE 1960) according to a technique devised by Dr. FOSTER B. CADY, Department of Statistics, Iowa State University. Use of a constant time interval as a base for measuring rates of photosynthesis and respiration introduced variation in the initial concentration of CO_2, but covariance analyses indicated no effect of differences in initial CO_2 over the range of initial concentrations used in this study.

Results

Net and gross photosynthesis of the aspen-poplar hybrids increased with light intensity up to 3,000 to 5,000 foot-candles and then decreased slightly or remained constant up to 6,000 foot-candles, the highest light intensity used in the study. Differences were apparent among light intensities in gross and net photosynthesis per plant and per gram of fresh and dry weight of leaf, and in net photosynthesis per sq. dm. of leaf (*Figs. 1 and 2* and *Table 1*). Differences in respiration among preceding light intensities were not significant.

Differences among clones were observed in net and gross photosynthesis per plant and per sq. dm. of leaf, and in net photosynthesis per gram of fresh and dry weight of leaf. Net photosynthesis of the Sherrill clone was greater than net photosynthesis of the Hansen and Crandon clones on a per plant basis, and greater than the Hansen clone on per gram of fresh and dry weight of leaf and per sq. dm. of leaf bases. Gross photosynthesis of the Sherrill clone was greater than gross photosynthesis of the Hansen and Crandon clones on a per plant basis and greater than the Hansen clone on a per sq. dm. of leaf basis. Gross photosynthesis of the Shimek clone was greater than gross photosynthesis of the Hansen clone on a per plant basis (*Figs. 3 and 4* and *Table 1*). Differences in respiration among clones were not significant.

Growth and distribution of assimilate of the aspen-poplar hybrids varied among clones (*Tables 2 and 3*). Because variations in fresh and dry weight were similar, only fresh weights are presented. In general, fresh and dry weight of total plant top, leaf, stem and root; length of stem; and leaf area of the Sherrill clone were greater than that of the Crandon and Hansen clones. Shimek, in general, surpassed the Hansen clone in fresh and dry weight growth, leaf area and shoot length. Conversely, number of roots of the Crandon clone was greater than number of roots of the Shimek and Hansen clones.

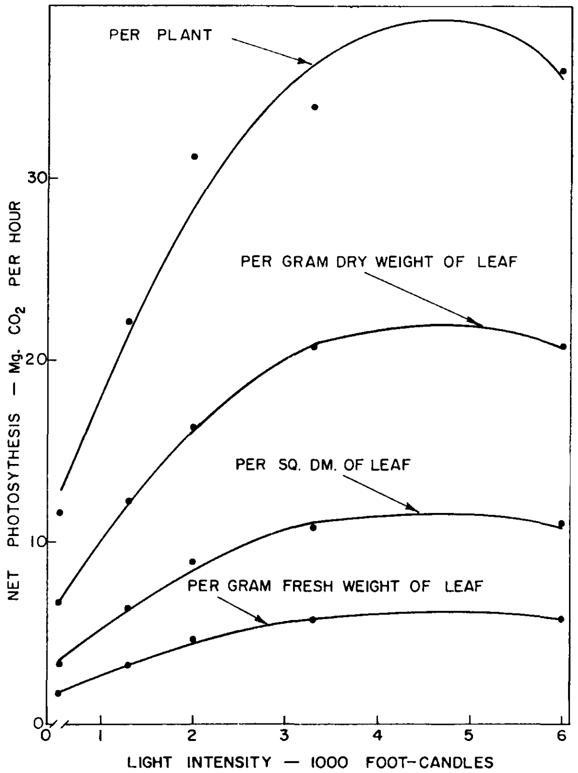

Figure 1. — Net photosynthesis of aspen-poplar hybrids in relation to light intensity, clones pooled.

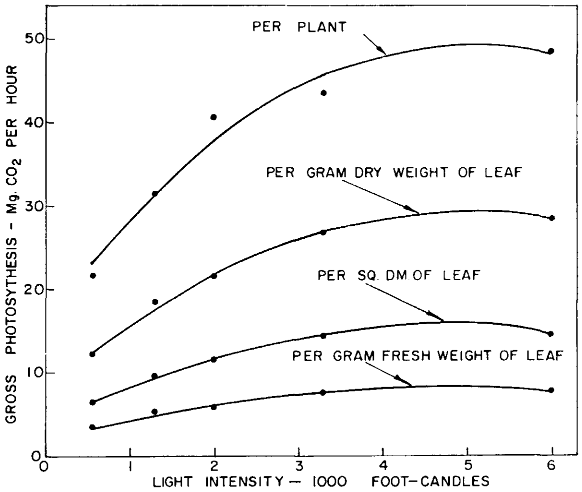

Figure 2. — Gross photosynthesis of aspen-poplar hybrids in relation to light intensity, clones pooled.

Table 1. — Mean squares from analyses of variance of net and gross photosynthesis of aspen-poplar hybrids.

Source	Replication	Light Intensity (L)				Error a	Clone (C)	L × C	Error b
df →	3	4	(Linear) (1)	(Quadratic) (1)	(Lack) (of fit) (2)	12	3	12	45
Net photosynthesis per seedling	448.35	1615.05*	3675.99*	2667.27*	58.48	260.27	736.81*	53.45	106.50
Net photosynthesis per g. fresh weight of leaf	6.59	46.17*	128.19*	55.96*	0.27	5.85	6.91**	2.13	2.14
Net photosynthesis per g. dry weight of leaf	98.32	581.39*	1657.14*	662.69*	2.86	66.77	116.12*	31.59	26.62
Net photosynthesis per sq. dm. of leaf	25.50	169.04*	460.06*	190.76**	2.67	20.99	39.65*	10.08	7.45
Gross photosynthesis per seedling	298.56	1798.92	3743.98*	3430.30*	10.70	235.96	776.10*	70.72	124.16
Gross photosynthesis per g. fresh weight of leaf	2.61	55.61*	147.94*	73.00*	0.74	4.69	2.35	2.93	2.65
Gross photosynthesis per g. dry weight of leaf	28.60	694.62*	1889.86*	860.55*	14.02	50.87	68.40	44.77	37.50

** Significant at 1% probability level.
* Significant at 5% probability level.

Distribution of assimilate, on a fresh and dry weight basis did not vary among the Sherrill, Shimek and Crandon clones but did vary between these clones and the Hansen clone. In the Hansen clone, more of the total assimilate was found in the top than in the root, and more of the assimilate in the top was found in the leaves than in the stem as compared with the Sherrill, Shimek and Crandon clones *(Table 3).*

Discussion

Differences do exist among clones and light intensities in rates of net and gross photosynthesis, but not in rates of dark respiration. No light intensity × clone interaction in rate of net photosynthesis was observed, thus indicating that the relative photosynthetic efficiency of the four clones is constant over a wide range of light intensities. Because light saturation for all clones appeared to occur at approximately 3,000 to 5,000 foot-candles, low survival and growth of field-planted stem cuttings probably is not related to the effect of light intensity on photosynthesis when they receive from 1/3 to 1/2 of full sunlight.

Table 2. — Mean squares from analyses of variance of growth of aspen-poplar hybrids.

Source	Replication	Clone	Error
df →	19	3	57
Fresh weight of top	4.49	33.73**	4.26
Dry weight of top	0.23	1.27**	0.30
Fresh weight of stem	0.59	5.29**	0.47
Dry weight of stem	0.02	0.23**	0.02
Fresh weight of leaves	2.36	12.89**	2.19
Fresh weight of roots	0.98	13.05**	0.57
Dry weight of roots	0.03	0.13**	0.01
Total fresh weight	9.94	82.54**	6.79
Total dry weight	0.36	1.99**	0.36
Stem length	7.38	167.47**	8.63
Root number	92.80	908.31**	49.76
Leaf area	0.46	1.52*	0.53

** Significant at 1% probability level.
* Significant at 5% probability level.

Inasmuch as light intensity treatments were applied only during the measurement of rates of photosynthesis at the end of the experiment, differences in plant size were not related to light intensity. Therefore, differences in rates of photosynthesis among light intensities were caused by differences in the uptake of CO_2 per unit of photosynthetic tissue (photosynthetic efficiency), not by differences in size.

Differences among clones in net and gross photosynthesis were related to differences in plant size and photosynthetic efficiency. However, the low correlation of net and gross photosynthesis per plant with total leaf area and weight and the high correlation with net and gross photosynthesis per unit of leaf area and weight, suggest that the differences among clones are primarily caused by differences in photosynthetic efficiency *(Table 4).* HUBER and POLSTER (1955) also found clonal differences in rates of photosynthesis per unit of leaf area of poplars. TONZIG and MARRÉ (1964) reported differences in photosynthetic activity among clones of pop-

Table 3. — Growth and distribution of assimilate of aspen-poplar hybrids in relation to clone.

Clone	Total Weight Fresh g	Top Weight Fresh g	Leaf Weight Fresh g	Stem Weight Fresh g	Root Weight Fresh g	Distribution of Assimilate							
						Top		Leaf		Stem		Root	
						Fresh %	Dry %	Fresh %	Dry %	Fresh %	Dry %	Fresh %	Dry %
Sherrill (C_2)	13.90	10.40	7.17	3.22	3.50	75	88	52	65	23	23	25	12
Shimek (C_4)	13.59	10.25	7.08	3.17	3.34	75	88	52	65	23	23	25	12
Crandon (C_3)	11.15	8.50	5.84	2.66	2.65	76	87	52	66	24	21	24	13
Hansen (C_1)	9.49	7.77	5.65	2.12	1.72	82	92	60	72	22	20	18	8

Clone	Leaf Area dm²	Shoot Length cm	Clone	Number of Roots
Shimek (C_4)	3.62	24.4	Crandon (C_3)	21.4
Sherrill (C_2)	3.56	22.2	Sherrill (C_2)	16.8
Hansen (C_1)	3.17	18.2	Shimek (C_4)	11.0
Crandon (C_3)	3.07	18.9	Hansen (C_1)	5.9

lar, as evidenced by increased production of xylem per unit of chlorophyll.

Because no differences in respiration occurred among preceding light intensities or clones, differences in net and gross photosynthesis appear to be caused by differences in CO_2 fixation by the photosynthetic process rather than by differences in the amount of CO_2 evolved in respiration. However, the validity of using CO_2 evolution as a measure of light respiration and the validity of using dark respiration as a measure of light respiration have both been questioned (Decker 1957, 1959, Krotkov *et al.* 1958).

Differences among clones in rates of photosynthesis provide an additional character that may be used as a basis for selection in tree improvement programs. The similarity between differences in early first-year growth and differences in rates of photosynthesis suggests that, in hybrids of this nature, rates of photosynthesis obtained in the laboratory may be used as production indices. However, for this hybrid, the correlation between rates of photosynthesis and total growth or wood production over a period of years has not been determined.

Differences do exist among clones in early first-year growth and distribution of assimilate. In general, the Sherrill and Shimek clones were superior to the Crandon and Hansen clones. Evidently, the Sherrill and Shimek clones are not only more efficient photosynthetically, they also are more efficient in the use for growth of stored food from stem cuttings. This superiority in the production and use of food in the first year argues strongly for the existence of metabolically superior genotypes within the aspen-poplar hybrid, the selection of which could be extremely beneficial in any tree improvement program. The poor performance of the Hansen clone may be directly related to its poor root development. Possibly the low rate of photosynthesis of the Hansen clone, coupled with a low rate of stored food mobilization, restricted root development in relation to initial shoot growth. The poorly developed root system, in turn, apparently restricted the amount of moisture and nutrients available for top growth, relative to the other three clones. Further investigation of the rooting habit of the Hansen clone in particular is necessary before it can be recommended for extensive field planting.

Table 4. — Correlation of net and gross photosynthesis per plant with total leaf area and weight and with net and gross photosynthesis per unit of leaf.

	Correlation Coefficients[1]	
	Net photosynthesis per plant	Gross photosynthesis per plant
Total leaf area	0.27*	0.26*
Leaf dry weight	0.26*	0.25*
Leaf fresh weight	0.22*	0.22*
Net photosynthesis per sq. dm. of leaf	0.92**	0.85**
Net photosynthesis per g. dry weight of leaf	0.92**	0.86**
Net photosynthesis per g. fresh weight of leaf	0.92**	0.86**
Gross photosynthesis per sq. dm. of leaf	0.80**	0.86**
Gross photosynthesis per g. dry weight of leaf	0.77**	0.84**
Gross photosynthesis per g. fresh weight of leaf	0.78**	0.85**

[1]) Degrees of freedom = 78.
** Significant at 1% probability level.
* Significant at 5% probability level.

Summary

Photosynthesis and respiration of seedlings of a naturally-occurring aspen-poplar hybrid (*Populus grandidentata* × *P. alba*) were determined for five light intensities and four clones, and growth and distribution of assimilate were determined for four clones. (1) Differences existed among

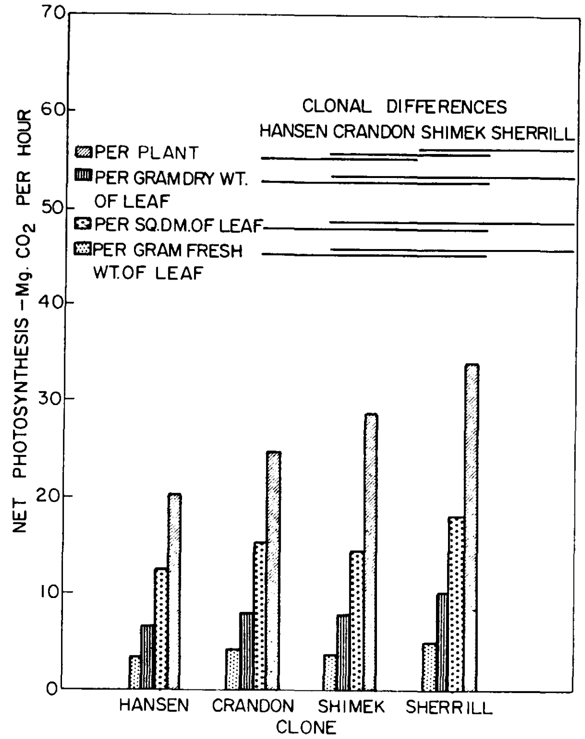

Figure 3. — Net photosynthesis of aspen-poplar hybrids in relation to clone, light intensities pooled. Net photosynthesis does not differ at the 1-percent level for clones grouped by a line.

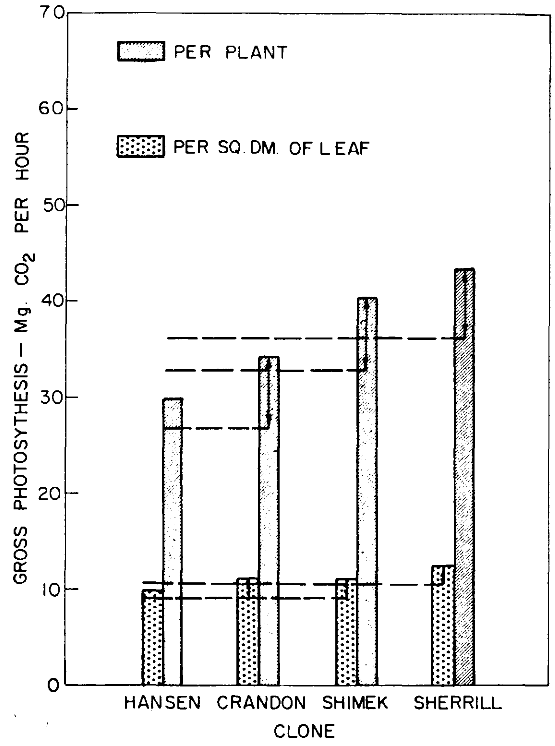

Figure 4. — Gross photosynthesis of aspen-poplar hybrids in relation to clone, light intensities pooled. Gross photosynthesis does not differ at the 5-percent level for clones grouped by an arrow.

clones and light intensities in rates of net and gross photosynthesis, but not in rates of dark respiration; (2) differences in rates of photosynthesis among light intensities were caused by differences in the uptake of CO_2 per unit of photosynthetic tissue (photosynthetic efficiency); (3) differences among clones in net and gross photosynthesis were related to differences in plant size and photosynthetic efficiency, but more closely to photosynthetic efficiency; (4) differences existed among clones in early first-year growth and distribution of assimilate; (5) differences among light intensities, with light saturation at approximately 3,000 to 5,000 foot-candles, indicate that low survival and growth of field-planted stem cuttings probably are not related to the effect of light intensity on photosynthesis when the seedlings receive ⅓ to ½ of full sunlight; (6) differences among clones in rates of photosynthesis provide an additional character that may be used as a basis for selection in tree-improvement programs; and (7) differences among clones from stem cuttings in early first-year growth and distribution of assimilate give strong evidence for the existence of metabolically superior genotypes, the selection of which could be extremely beneficial in any tree improvement program.

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Linkage Between Marker Genes and Embryonic Lethal Factors May Cause Disturbed Segregation Ratios

By Frank Sorensen[1]

(Received for publication August 2, 1966)

Several recent papers have reported ratios of normal to deviant or marked seedlings after self-pollination of trees of coniferous species. The range of reported ratios is from 2.2 : 1 (Squillace and Kraus 1963) to 18.8 : 1 (Fowler 1965 c), with many of them clustered around the 3 : 1 monohybrid segregation ratio, or somewhat higher at 4 to 10 : 1.

It has seldom been clear why the observed ratios often differed considerably from the expected 3 : 1 for marker traits, although several causes have been suggested. These have been:

1. Deviant seedlings difficult to identify, perhaps because mutant trait sensitive to environment.
2. Sampling error. Most selfed families are small and observed ratios such as 2.2 : 1 and 4 or 5 : 1 do not differ significantly from the expected 3 : 1 ratio.
3. More than one genetic factor may underlie the trait.
4. Embryo abortion after one fertilization per ovule. Many deviant seedlings are weak as seedlings. Therefore, it is not unreasonable to expect that they were weak as proembryos or embryos also and that a proportion may have succumbed before germination. In other words, the deleterious effect of the marker mutant may be pleiotropic as well as direct.
5. Pregermination selection after multiple fertilization. Multiple fertilization has been verified in some coniferous species (Sarvas 1962, p. 94) and more than one embryo commences growth within a single gametophyte. If a deviant (homozygous recessive) embryo is competing with a normal embryo in this situation, the deviant embryo may be selected against. This has occurred in *Pinus resinosa* Ait. (Fowler 1964).

Any of these reasons may be valid. However, there is a fifth possible cause of deviation from the monohybrid ratio — linkage between the marker and a gene which somehow prevents germination (an embryonic lethal gene). For example, if a tree is heterozygous for both a recessive marker gene (selectively neutral) and a recessive embryonic lethal gene, and if the two recessives are completely linked in coupling, a selfed progeny from this tree will contain no marked seedlings. Only normals would germinate. Another example: if the two genes are completely linked in repulsion, a selfed progeny will contain normal-to-deviant seedlings in the proportion of 2 : 1. Now, none of the aborting embryos would carry the marker gene as homozygous recessive; all deviant individuals would germinate. Of

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