were not yet reprogrammed in one or both retinal axes by stage 43/44 (separation after 30 to 32 hours fusion); yet reprogramming in both axes was observed in the temporal retina of all recombinant eyes. This suggests that reprogramming can occur at least as late as stage 44, well into larval life.

The discovery of a stable intermediate in reprogramming (both axes inverted) is particularly telling, in that it virtually excludes wholesale "derotation" of the retinal field (*12, 13*) as the mechanism of axis reversal, and shows that the retina never reverts to a completely blank intermediate state. The curvature of only one axis, when only one axis has been reprogrammed (Fig. 1d), also shows that the two reference axes for position-dependent differentiation need not be strictly orthogonal. That the AP axis is reprogrammed first (even though it is the DV axis which is misaligned) provides strong support for the hypothesis (*12*) that the transmission or processing (or both) of AP signals is more rapid than that of the DV signal. Yet, DV misalignment may help to trigger the AP reprogramming, for recombinant eyes comprised of a right-temporal fragment and a right-nasal fragment nearly always integrate to form a single normal pattern (*12, 14*).

Finally, this work introduces what we hope will be a powerful assay system for analysis of positional signaling within the retina and for polarity transforms in general. Evidence is presented elsewhere that the reprogramming is highly specific and determined by the axial relations in the retinal fragments. Thus, the system provides an anatomically defined source of axial signals that can be independently perturbed. Moreover, by examining their abilities to reprogram normal fragments, it may now be possible to analyze the axial relations and specified state of experimental eyes submitted to procedures that preclude the recovery of normal visual function.

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Photosynthate and Nitrogen Requirements for Seed Production by Various Crops

Abstract. *Seed biochemical composition was the basis for segregating 24 crops into four distinct groups. Nitrogen requirements of pulses and soybeans were so great that sustained seed growth demanded continued nitrogen translocation from vegetative tissues. This translocation must eventually induce senescence in these tissues, restrict the duration of the seed-fill period, and limit seed yield.*

Seeds of crop species vary a great deal in their chemical composition and these differences significantly influence their utility to man. The formulations of livestock feed or the diets of humans, for example, are based to a great extent on the relative proportions of protein, carbohydrate, and lipid of the various available grains. Recently, attempts have been made through crop breeding to alter the chemical composition of seeds and thereby enhance their nutritional and economic value.

However, the impact of altering the chemical composition of seeds on the photosynthate and nitrogen relationships within the crop plant and, consequently, on crop productivity have rarely been considered. It has long been known that the caloric values of protein, carbohydrate, and lipid are quite different. Assuming the leaves of a crop produce photosynthate at a fairly uniform rate and hence yield a constant caloric output, it necessarily follows that changes only in the chemical constituents of seeds must alter biomass yield. An objective of this analysis was to compare the biomass yield per unit of photosynthate of seeds having different relative amounts of protein, carbohydrates, and lipid. In addition, altering the protein content of seeds also changes the amount of nitrogen required in the production of seed biomass. Since nitrogen fertilization is recognized as a critical factor in crop production, changes in nitrogen demand resulting from alterations of seed composition may require a reevaluation of management techniques for crop nitrogen supplies. Therefore, a second objective of this analysis was to examine the nitrogen requirements of seeds with varying protein contents.

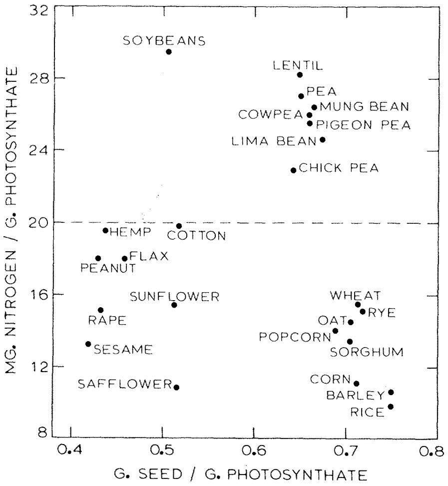

Fig. 1. Plot of milligrams of nitrogen required and grams of seed biomass yielded per gram of available photosynthate for the 24 crop species analyzed. The dashed line represents the nitrogen requirement when the nitrogen supply rate is 5 g ha^{-1} day^{-1} and the available photosynthate rate is 250 kg ha^{-1} day^{-1}.

The relative amounts of protein, carbohydrates, lipid, and ash (on the basis of fresh weight) of 24 crop seeds were used in this analysis (*1*). All data were first converted to dry weight and a wide range in the relative composition of seeds was obtained (see Table 1). The ranges for the relative amount of protein, carbohydrate, and lipid were 8 to 38 percent, 19 to 88 percent, and 1 to 54 percent, respectively. While the data for a given species may be unrepresentative of some genotypes within the species, the range in these data allows evaluation of the seed biomass production and nitrogen requirements of cultivars with differing chemical compositions.

The relative seed compositions were first used to calculate the photosynthate requirements for biomass production. The results of an exhaustive examination of the biochemical pathways for the production of proteins, carbohydrates, and lipids from glucose by Penning de Vries (*2*) were used. His analysis showed that the biomass conversions were, in fact, fairly insensitive to the synthesis pathway and the subcomponents of the end products. He found that from 1 unit of glucose about 0.83 unit of carbohydrates, 0.40 unit of protein (assuming nitrate to be the nitrogen source), or 0.33 unit of lipid could be produced. Knowing the relative composition of the seeds and these constituent conversions, we tabulated a conversion coefficient for the production of whole seed from glucose for each species. These data, expressed as grams of seed biomass produced per gram of photosynthate (that is, glucose), are presented in Table 1. More detailed calculations are required to account for nitrogen supplied to the seeds by redistribution from the vegetative tissues, which is not nitrate.

The nitrogen required by the seed was also tabulated by first calculating the mass of protein produced per unit mass of available photosynthate. We assumed protein was 15 percent nitrogen by weight in order to estimate the milligrams of nitrogen required per gram of photosynthate for each species (see Table 1).

These calculations resulted in yield estimates of seed biomass from 1 g of photosynthate ranging from 0.42 g for sesame to 0.75 g for barley and rice, which suggests an almost twofold difference in seed yield even when the photosynthetic productivities of the crops are equal. Similarly, a wide range of nitrogen requirements were calculated among the crops. Rice had the lowest demand, requiring only 10 mg of nitrogen per gram of photosynthate, while soybean was the highest with a requirement of 29 mg of nitrogen per gram of photosynthate. This threefold difference is not as large as the difference in protein content among the crops, but significant variability among species in their nitrogen requirements is suggested.

Table 1. Chemical composition, biomass productivity (grams of seed per gram of photosynthate), and nitrogen requirement (milligrams of nitrogen per gram of photosynthate) of seeds of 24 crop species.

Species	Composition (percentage of dry weight)				Biomass productivity (g/g)	Nitrogen requirement (mg/g)
	Carbohydrate	Protein	Lipid	Ash		
Barley (*Hordeum vulgare*)	80	9	1	4	0.75	11
Bean, lima (*Phaseolus vulgaris mac.*)	70	24	2	4	0.67	25
Bean, mung (*Phaseolus aureus*)	69	26	1	4	0.66	26
Chick pea (*Cicer arietinum*)	68	23	5	4	0.64	23
Corn (*Zea mays*)	84	10	5	1	0.71	11
Cotton (*Gossypium hirsutum*)	47	25	25	3	0.52	20
Cowpea (*Vigna sinensis*)	69	26	2	3	0.66	26
Flax (*Linum usilatissium*)	32	26	38	4	0.46	18
Hemp (*Cannabis sativa*)	27	29	41	3	0.44	20
Lentil (*Lens culinaris*)	67	28	1	4	0.65	28
Oat (*Avena sativa*)	77	13	5	5	0.70	14
Pea (*Pisum sativum*)	68	27	2	3	0.65	27
Peanut (*Arachis hypogaea*)	25	27	45	3	0.43	18
Pigeon pea (*Cajanus cajan*)	69	25	2	4	0.66	26
Popcorn (*Zea mays praecox*)	80	13	5	2	0.69	14
Rape (*Brassica napus*)	25	23	48	4	0.43	15
Rice (*Oryza sativa*)	88	8	2	2	0.75	10
Rye (*Secale cereale*)	82	14	2	2	0.72	15
Safflower (*Carthamus tinctorius*)	50	14	33	3	0.52	11
Sesame (*Sesamum indicum*)	19	20	54	7	0.42	13
Sorghum (*Sorghum vulgare*)	82	12	4	2	0.70	13
Soybean (*Glycine max*)	38	38	20	4	0.50	29
Sunflower (*Heliantus annus*)	48	20	29	3	0.51	15
Wheat (*Triticum esculentum*)	82	14	2	2	0.71	16

To visualize more easily the differences among the crops, the nitrogen requirements per gram of photosynthate were plotted in Fig. 1 against biomass production per gram of photosynthate. The crops segregated into four distinct groups. In the lower right-hand quadrant of Fig. 1 are the grain-cereal crops that have been traditionally the world's staple crops. These seeds are characterized by low protein and lipid contents. In the lower left-hand quadrant is a slightly more scattered group of crops containing most of the world's oil crops, which have the common characteristic of high lipid contents. Their yields are only about 60 percent of the grain yields, which is in good agreement with the yield ratio of rape seed and wheat in the Netherlands. The upper right-hand quadrant contains crops that are low in lipid content but have fairly high protein contents. This group contains many of the pulse crops grown for human consumption. Soybeans are the sole crop in the remaining quadrant, which demonstrates its uniqueness among the world's crops in both the composition of its seed and potential limitations to its productivity. Soybeans not only require the greatest amount of nitrogen in seed production but are also one of the lowest producers of seed biomass per unit of photosynthate.

By assuming rates of crop photosynthate production and nitrogen uptake from the soil, further distinctions among the crop species can be made based on the nitrogen balance. We estimate that healthy, adequately fertilized crops will produce photosynthate for seed production at a rate of about 250 kg ha^{-1} day^{-1}. A nitrogen uptake rate of 5 kg ha^{-1} day^{-1} is in the range of maximal uptake rates for many crops. Division of the estimated nitrogen uptake rate by the photosynthate production rate yields an estimate of the nitrogen supply to the seed from the soil of 20 mg of nitrogen per gram of photosynthate. This nitrogen supply, shown as the horizontal dashed line in Fig. 1, is sufficient only to satisfy the nitrogen demands of the crops in the two lower quadrants. The species in the top part of Fig. 1 are not able to meet the total nitrogen demand generated by the seed from the nitrogen supplies available from the soil. Increasing the nitrogen uptake rate to 6 kg ha^{-1} day^{-1} increases the supply to 24 mg of nitrogen per gram of photosynthate and leaves the division between the crop groups nearly unaffected, with only chick pea moving below the line.

For the crop species in the top part of Fig. 1 to sustain the calculated rates of seed biomass production, we hypothesize that the remaining nitrogen demand must be obtained from the vegetative plant parts. Experimental observations of nitrogen mobilization and translocation from leaves to seeds during seed development support this hypothesis (*3*). Since the pool of nitrogen and protein in vegetative tissues will be continually depleted, the vegetative tissues must eventually lose physiological activity as the nitrogen levels decrease and the plant becomes "self-destructive." Many of these self-destructive species in the top part of Fig. 1 exhibit leaf senescence and abscission during seed development. Final seed yield of these species may also be closely tied to the self-destructive characteristic. Since the duration of the seed development period is obligatorily linked to productive vegetative tissues, if seed development eventually impairs the physiological activity of vegetative tissues, seed production in the self-destructive species is inherently limited to a finite length of time for seed-fill. Therefore, the duration of the seed development period is intimately tied to the rate of nitrogen uptake by the self-destructive crop during seed-fill. A low rate of uptake results in a large nitrogen demand and leads to extensive nitrogen translocation to the seeds from vegetative tissue, a shorter period of seed development, and lower total yield (*4*).

We expect that the self-destructive species would be unresponsive to nitrogen fertilization unless it increased directly the rate of nitrogen uptake by the plant during seed-fill. The inability of the self-destructive crops to respond to nitrogen fertilizer is aggravated because many of these species support symbiotic nitrogen fixation, which tends to decrease in proportion to nitrogen fertilization. In soybeans the yields of a nodulating genotype were essentially unchanged by nitrogen fertilization, while the yields of a nonnodulating isoline increased with fertilization, reaching those of the nodulating genotype (*5*).

For the species in the lower portion of Fig. 1 seed growth may be sustained by a relatively small rate of uptake of nitrogen during the seed-filling period without the necessity of nitrogen redistribution within the plant. However, these species may also translocate nitrogen during seed development and the total amount of nitrogen available from the soil is often finite, so that self-destruction may also develop in the species in the lower portion of Fig. 1. Nitrogen fertilization may at least partially alleviate the limitation of nitrogen availability in the soil and minimize the effects of the self-destructive process in these species. This agrees with the well-established phenomenon that nitrogen fertilization of small grains increases yield by postponing senescence.

Our analysis of the chemical composition of crop seeds shows the potential importance of nitrogen availability and supply on crop yields. The seed yields of crop species identified as self-destructive may be significantly inhibited by insufficient rates of nitrogen supply. The high rates of nitrogen uptake demanded by the seeds of these species may cause the rapid translocation of nitrogen from the vegetative plant parts. The destruction of proteins in vegetative plant parts leads to a loss in physiological activity and senescence of the plant, and a shortened period for seed development. The remaining species are not generally limited by the potential rate of nitrogen supply from the soil but rather the total amount of available nitrogen.

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Rapid Food-Aversion Learning by a Terrestrial Mollusk

Abstract. *The terrestrial slug* Limax maximus *can learn to avoid new palatable food if* CO_2 *poisoning is paired with ingestion of the new food. Some animals learn in one trial and remember without error for 3 weeks. Avoidance most commonly consists of complete rejection of the unsafe food, based on olfactory cues. This preparation offers the opportunity for detailed neurophysiological analysis of a rapid-onset learning mechanism of long duration.*

There are specialized mechanisms which provide for very rapid and long-lasting learning. Imprinting and song-learning by birds are classical examples. Such rapid learning has been documented for invertebrates in studies of wasp nest-site recognition (*1*), honey bee communication (*2*), and octopus visual discrimination tests (*3*). Because invertebrate preparations are proving increasingly useful in studies of the cellular basis of learning (*4*), it would be advantageous to document a rapid-onset learning mechanism of long duration in an invertebrate whose nervous system is amenable to detailed neurophysiological analysis. The terrestrial slug, *Limax maximus*, is such an organism (*5*).

Several species of vertebrates, including man, possess a specialized learning mechanism which can associate food-related sensory cues with the internal consequences of ingestion. Rats will rapidly and specifically associate a new odor or taste with intestinal malaise produced experimentally (*6*). Such learning shows a rapid onset, high resistance to extinction, specificity to olfactory and gustatory inputs, occurrence with long (> 1 hour) delays between sensory input and internal consequence, and resistance to disturbance by electroconvulsive shock (*7*). Birds have a similar learning mechanism but use visual cues to form aversions to new foods associated with gastric upset (*8*).

The terrestrial pulmonate slug, *Limax maximus*, is a generalized herbivore faced with the problem of assessing both nutritional value and potential toxicity of foods. The selectivity of food plant selection by wild slugs has been amply demonstrated. Gain (*9*) offered *Limax* 194 different food items, of which 155 (80 percent) were totally rejected. Preferences for the 39 acceptable foods varied, with mushroom (*Boletus edulis*) and carrot root (*Daucus carota*) being most avidly eaten. Frömming (*9*) showed that *Limax* would accept only 31 percent of 110 varieties of higher plants. Potato tubers (*Solanum tuberosum*) and cucumber seed pods (*Cucumis sativa*) were eaten more readily than any of the other plant leaves, roots, or fruits offered. Below