heavy chain classes than in the light chain types.

The hypothesis of a common evolutionary origin of light and heavy chains is supported by the sequence data for human μ-chains. Eight of the first 27 residues of a typical human λ-chain are identical with corresponding positions in the three heavy chains in Fig. 1; other positions are identical with those in one or more of the heavy chains. A similar homology is shown when corresponding portions of human λ- and κ-chains are compared to the sequence of the F3 fragment of the human μ-chain (Fig. 1). In support of the suggestion (*18*) that haptoglobins also evolved from a primitive light chain precursor, a weak homology exists when the sequence of the human haptoglobin α^1-chain is compared to that of the κ-, λ-, and μ-chains.

More structural data on γ-, α-, and μ-chains of several species will be required before the phylogenetic and evolutionary considerations proposed above can be verified. Complete sequence data on individual γ- and μ-chains of the same species are needed to fix the location of the variable and constant portions of heavy chains and to ascertain the extent of the variability in sequence.

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Photosynthesis: Temperate and Tropical Characteristics within a Single Grass Genus

Abstract. *Leaves of two subgenera of* Panicum *differ in photosynthetic physiology and bundle sheath characteristics. Species of the subgenus Eupanicum, like other tropical grasses, had high phosphoenolpyruvate carboxylase (E.C. 4.1.1.31) activity, had specialized chloroplasts within the parenchyma bundle sheath cells, and lacked photorespiration. The pattern for the temperate subgenus Dichanthelium was opposite.*

Tropical grasses can fix carbon dioxide at a rate almost twice that of temperate species (*1*). The lower photosynthetic rate of temperate leaves is probably a result of photorespiration, because blocking this process by lowering the ambient oxygen concentration (*2*) can increase the rate of photosynthesis to approximately that of tropical leaves (*3*). Temperate plant yields can also be increased substantially under these conditions (*4*). Consequently genetic selection for greater carbon conservation during photosynthesis as a means of increasing dry matter production among temperate grass crops is particularly attractive. At the same time, the introduction of temperate or tropical characters into species of the opposite type may extend their range of cultivation.

To date we have been unable to test these possibilities because of the lack of variability within a phylogenetic line. That is, genera belonging to the same phylogenetic group have basically the same photosynthetic physiology and internal leaf anatomy. Therefore we have been interested in species of any groups reported to have characteristics that are in apparent disagreement with former correlation data (*5*). The report (*6*) that parenchyma bundle sheath cells of the rosette leaves of *Panicum lindheimeri* do not contain "specialized starch plastids typical of the tribe" was valuable in this regard. This species belongs to the subgenus Dichanthelium, a group of more than 100 species confined chiefly to eastern North America (*7*). Since our previous survey considered only members of the largely tropical subgenus Eupanicum, we have extended it to include some dichantheloid species. It is evident that two different functional patterns exist within this economically important genus.

Photorespiration was estimated by measuring the carbon dioxide compensation point of detached leaves. They were illuminated at 33,000 lu/m^2 in a closed system, and their gas exchange was monitored by an infrared carbon dioxide analyzer. Those leaves that evolved carbon dioxide during photosynthesis reached an equilibrium carbon dioxide concentration (compensation point) of approximately 50 ppm. Species lacking photorespiration compensated at 5 ppm or less (*5*, *8*). To determine initial photosynthetic products, leaves were illuminated at 11,000 lu/m^2 and then exposed to $^{14}CO_2$ in air for 6 seconds; they were then killed and extracted in boiling 80 percent ethanol. Compounds were resolved on paper strips with a liquified phenol, acetic acid, water, 1*M* ethylenediaminetetraacetic acid system (840 : 160 : 10 : 1) (*9*). A chromatogram scanner was used to measure the amount of ^{14}C incorporated into photosynthetic intermediates. Phosphoenolpyruvate (PEP) carboxylase (E.C. 4.1.1.31) activity was assayed according to Slack and Hatch (*10*). Free-hand cross sections of leaves were examined microscopically for anatomical detail. Addition of iodine–potassium iodide to the water mount indicated the areas of starch accumulation.

Members of the subgenus Eupanicum, such as *Panicum bulbosum*, *P. capillare*, and *P. miliaceum*, like other species of the panicoid and chloridoid–

eragrostoid lines of phylogeny, formed C_4 dicarboxylic acids (malate, aspartate, and oxaloacetate) as initial photosynthetic products, but did not evolve carbon dioxide by photorespiration (*5, 11*). The amount of ^{14}C incorporated into aspartic and malic acids ranged from 85 to 92 percent of the total ^{14}C fixed. Consistent with this, leaves of *Panicum miliaceum* contained much PEP carboxylase activity (28.15 μmole of CO_2 fixed per milligram of extractable chlorophyll per minute). This enzyme is used for the synthesis of C_4 compounds (*10*). The parenchyma bundle sheath was extensively developed and contained large starch-laden chloroplasts. The mesophyll cells accumulated little starch.

The dichantheloid species, *Panicum commutatum, P. lindheimeri,* and *P. pacificum,* like the previously studied temperate grasses, synthesized phosphorylated compounds typical of the Calvin cycle, as major products of carbon dioxide fixation (*11*). Phosphorylated compounds accounted for 86 to 95 percent of the total ^{14}C fixed. The leaves also had an active photorespiratory pathway manifested by the evolution of carbon dioxide during photosynthesis (*5*). As expected (*10*), leaf extracts of *Panicum pacificum* had low PEP carboxylase activity (3.16 μmole of CO_2 fixed per milligram of extractable chlorophyll per minute). This value was virtually identical to that found for wheat leaves. Unlike many temperate grasses, however, leaves of the subgenus Dichanthelium contained extensively developed parenchyma bundle sheaths. Despite this elaboration, chloroplasts were absent from the tissue. Leaves of the rosette, vernal, and autumnal growth phases were similar in structure and photosynthetic physiology.

The absence of detectable photorespiration in plants of tropical origin could result from a deficiency of the pathway found in temperate species (*12*), or from a mechanism that prevents carbon dioxide loss. The great affinity of PEP carboxylase for carbon dioxide is well known (*13*). The high activity of this enzyme in tropical plants might preclude the release of carbon dioxide to the outside of the leaf. The specialized chloroplasts within the parenchyma bundle sheath could also be a determinant. Whatever the correct explanation may be, the important point is that tropical grass species do not lose carbon during photosynthesis and temperate species do. The discovery of different physiological and cytological phenotypes within the same genus may now permit genetic analysis of photorespiration and assessment of its importance to the carbon budget of the plant.

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Induction of Brain D(—)-β-Hydroxybutyrate Dehydrogenase Activity by Fasting

Abstract. *D(−)-β-hydroxybutyrate dehydrogenase activity is very low in normal adult rat brain; but during fasting it increases severalfold in parallel with the ketosis. The increase may represent part of a mechanism by which the brain adapts to changing patterns of substrate supply during starvation.*

Owen *et al.* (*1*) have observed that, in obese human subjects after a 5 to 6 week fast, the brain uptake of β-hydroxybutyrate and acetoacetate assumes significant proportions. If completely oxidized to carbon dioxide and water, these metabolites would have accounted for 60 percent of the total cerebral oxygen consumption—52 percent by β-hydroxybutyrate alone—whereas glucose utilization would have required at most only 29 percent of the oxygen uptake. This is in marked contrast to the situation in normal adult brain in which ketone bodies are only negligibly utilized and glucose uptake accounts for almost all the oxygen consumed (*2*). There is, in fact, considerable evidence that no substrate other than glucose can be oxidized sufficiently rapidly by mature brain to maintain its normal energy metabolism and function (*2*). Immature brain may be different. Drahota *et al.* (*3*) have observed that acetoacetate can support nearly the same rate of oxygen consumption as glucose in cerebral cortical slices from 5-day-old rats. Recent studies in our laboratory (*4*) have revealed high levels of activity of the mitochondrial enzyme, D(−)-β-hydroxybutyrate dehydrogenase (E.C. 1.1.1.30, D-3-hydroxybutyrate: NAD^+ oxidoreductase) (BDH) in brains of unweaned rats, but the enzyme activity declines to very low levels when the brain matures. The question then arises how, in view of the apparent limited ability of the normal mature brain to oxidize substrates other than glucose and of its low D(−)-β-hydroxybutyrate dehydrogenase activity, β-hydroxybutyrate utilization could reach such high levels in the brains of the fasting adult patients studied by Owen *et al.* (*1*). Our results demonstrate that fasting leads to an increase in D(−)-β-hydroxybutyrate dehydrogenase activity in adult brain.

We used normal adult male Sprague-Dawley rats approximately 8 months of age and having a mean weight ± standard error of 580 ± 24 g. The animals were housed in individual wire cages; they were allowed free access to Purina Laboratory Chow for 2 weeks before the study began and free access to water at all times. Daily intraperitoneal injections of their minimal daily requirements of thiamine, riboflavin, niacinamide, pyridoxine, and pantothenic acid (*5*) were instituted 1 week before the beginning of fasting. The study was begun by the initiation of fasting; all food (but not water) and feces were removed from the cages at 9:00 a.m. of the selected day. At various times after