

Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel

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ABSTRACT

Carbon isotope ratios ($\delta^{13}\text{C}$ values) of herbivores reflect the $\delta^{13}\text{C}$ values of dietary plants, and the $\delta^{13}\text{C}$ values of grazers (animals that consume >90% grass) reflect the local abundance of C_3 versus C_4 grasses. Because grassland C_3/C_4 ratios correlate with climate, the $\delta^{13}\text{C}$ of fossil grazers may serve as a proxy for reconstructing paleoclimates and paleovegetation patterns. However, the accuracy of environmental reconstructions based on herbivore $\delta^{13}\text{C}$ values is often uncertain, because the relationship between the $\delta^{13}\text{C}$ of many animals and the abundance of C_4 and C_3 grasses has not been precisely quantified. We analyzed the $\delta^{13}\text{C}$ of tooth enamel carbonate from modern bison (*Bison bison*) from nine localities in the United States. The C_4 grass biomass at these sites ranged from <1% to ~95% of the total grass biomass. The mean $\delta^{13}\text{C}$ of enamel for each population correlated well with the local abundance of C_4 grasses and with variations in mean annual temperatures. The variability of enamel $\delta^{13}\text{C}$ values did not differ among habitats and was not correlated with the abundance of C_4 grasses. These results demonstrate that analyses of the $\delta^{13}\text{C}$ values of fossil bison can be used as a quantitative proxy for reconstructing grassland C_3/C_4 ratios and paleotemperatures, and they will serve as a baseline for interpreting the $\delta^{13}\text{C}$ of fossil bison and other large herbivores in North America.

Keywords: *Bison*, carbon isotopes, enamel, diet, grasslands.

INTRODUCTION

Analyses of fossil bison hold promise for use as a quantitative paleoenvironmental proxy in North America because (1) direct measurements of the isotopic fractionation between modern bison and their environments can serve as a good analog for fossil species (Tieszen, 1994); (2) bison $\delta^{13}\text{C}$ values should correlate with the mean $\delta^{13}\text{C}$ values of local grasslands, because bison are selective feeders that usually consume >90% graminoids (grasses and sedges) (Tieszen, 1994; Coppedge et al., 1998); (3) bison occur in high abundance in fossil and archaeological deposits (Frison, 1991); (4) prehistoric bison had a wide geographic range (from Alaska to Mexico).

Analyses of wild herbivores (Cerling and Harris, 1999) and feeding experiments on domestic cattle (Passey et al., 2005) have demonstrated that bovid tooth enamel $\delta^{13}\text{C}$ values are fractionated $+14.6 \pm 0.3\text{‰}$ relative to dietary plants. The $\delta^{13}\text{C}$ value of plants varies primarily with photosynthetic pathways and, to a lesser extent, with changes in climatic and environmental conditions (Farquhar et al., 1989). Most trees, herbs, and cool-season grasses use C_3 photosynthesis, which produc-

es tissues averaging $-27 \pm 3\text{‰}$. Warm-season grasses use C_4 photosynthesis and average $-13 \pm 2\text{‰}$ (Tieszen and Boutton, 1989). The enamel of modern animals with pure C_3 and a pure C_4 diet averages -13‰ and 1‰ , respectively (Cerling et al., 1997). Thus, the $\delta^{13}\text{C}$ of fossil grazers can be used to reconstruct gradients in the abundance of C_4 grasses (e.g., Cerling et al., 1997). Furthermore, because the percentage of C_4 grass biomass in grasslands correlates with changes in temperature and precipitation (Paruelo and Lauenroth, 1996; Epstein et al., 1997), the $\delta^{13}\text{C}$ of fossil herbivores may also serve as a paleoclimatic proxy (Connin et al., 1998; Lovvorn et al., 2001).

The $\delta^{13}\text{C}$ of modern bison tooth enamel, bone collagen, feces, and horn keratin reflects latitudinal patterns in the distribution of C_3 and C_4 grasses (Tieszen, 1994, 1998; Steuter et al., 1995; Larson et al., 2001; Feranec, 2004). However, the relationship between the $\delta^{13}\text{C}$ of bison tissues and the abundance of C_4 grasses has not been quantified, and the scale of intrapopulation variability has not been documented. Studies that use the $\delta^{13}\text{C}$ values of bison to examine paleobiology, grassland paleovegetation patterns, or paleoclimatic changes (Chisholm et al., 1986; Connin et al., 1998; Gadbury et al., 2000; Larson et al., 2001; Lovvorn et al., 2001) use isotopic fractionation measured in other species. Thus, the

accuracy of paleovegetation reconstructions based on bison $\delta^{13}\text{C}$ values is currently uncertain.

Interpreting herbivore $\delta^{13}\text{C}$ values is complicated by the fact that grazers often consume some C_3 herbs and/or shrubs and because the amount of C_3 plants consumed can differ among animals within a population. These factors can result in errors of >40% when calculating the C_4 abundance on the basis of fossil $\delta^{13}\text{C}$ values (Hoppe et al., 2005). Fecal analyses of modern bison suggest that they consume <10% browse plants, but bison from mixed C_3/C_4 grasslands may preferentially feed seasonally on either C_3 or C_4 grasses (Tieszen, 1998; Coppedge et al., 1998). In addition, the different parts of a plant (e.g., protein vs. lipids) can display different $\delta^{13}\text{C}$ values, and the average $\delta^{13}\text{C}$ values of a plant can change seasonally by 0.5‰ (Tieszen and Boutton, 1989); animals that selectively feed on only part of a plant or those that change their feeding pattern seasonally may display different $\delta^{13}\text{C}$ ratios. These differences are most pronounced for highly selective feeders such as insects and rodents, but they emphasize that quantitative relationships derived for one species are not always directly applicable to another species.

METHODS

We collected teeth from modern bison that inhabit native grasslands ecosystems that have never been plowed and are located from latitude 35° to 47°N and longitude 96° to 114°W (Fig. 1; Table DR1¹). Powdered enamel samples that represent 1 yr of growth were collected from the third molar, which mineralizes after weaning (Gadbury et al., 2000; Zazzo et al., 2005). Samples were pretreated according to methods described in Koch et al. (1998). Analyses were conducted on a Finnigan Delta Plus XE isotope ratio mass spectrometer equipped with a Gas Bench II sample preparation device. Calcite standards were referenced to NBS-19 and had a precision of

¹GSA Data Repository item 2006133, Table DR1 (climate, mean $\delta^{13}\text{C}$ of enamel, and measured percentage of C_3/C_4 grass biomass at field locations) and Table DR2 ($\delta^{13}\text{C}$ values of enamel from individual bison), is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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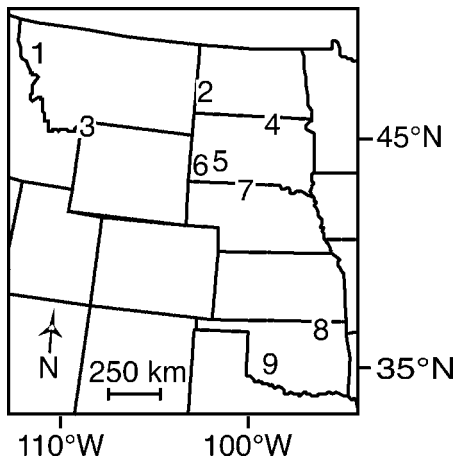


Figure 1. Locations of modern bison herds. 1—National Bison Range; 2—Theodore Roosevelt National Park; 3—Yellowstone National Park; 4—Ordway Prairie Preserve; 5—Badlands National Park; 6—Wind Cave National Park; 7—Fort Niobrara National Wildlife Refuge; 8—Tallgrass Prairie Preserve; 9—Wichita Mountains National Wildlife Refuge.

$\pm 0.2\text{‰}$ (1σ). Duplicate samples ($n = 26$) displayed a mean difference $< 0.2\text{‰}$. Results are reported in standard delta (δ) notation relative to the PDB (Peedee belemnite) standard.

Enamel $\delta^{13}\text{C}$ values were compared to measurements by other authors of the contribution of C_4 grass biomass to the total above-ground grass biomass at the same site or nearby sites ≤ 40 km distant (Table DR1; see footnote 1). Biomass measurements are based on vegetation surveys, species identification of harvested material, and isotopic analyses (Lomasson and DeNio, 1940; Sims et al., 1978; Iowa Cooperative Wildlife Research Unit, 1981; Tieszen et al., 1988; Tieszen, 1994; Steuter et al., 1995; Follett et al., 1997; Tieszen et al., 1997; Feranec, 2004). Because measurements of grassland biomass were not available for the Wichita Mountains National Wildlife Refuge, we used an estimate of C_4 abundance based on the $\delta^{13}\text{C}$ of grassland soil carbonates (84%) (Follett et al., 1997), which was consistent with modeled and remote sensing measurements of the C_4 grassland production for this region (80%–90%) (Tieszen et al., 1997). Although the Wichita Mountains support a mixture of open woodlands and mixed-grass prairie, bison do not spend a significant amount of time feeding in woodland environments (K.J. Kimball, 2006, personal commun.).

RESULTS

Because the $\delta^{13}\text{C}$ value of atmospheric CO_2 has changed since the industrial revolution (by $> 1\text{‰}$) owing to the burning of fossil fuels (see Marino and McElroy, 1991), older specimens have $\delta^{13}\text{C}$ values that are offset relative to their modern counterparts (e.g., Cerling and

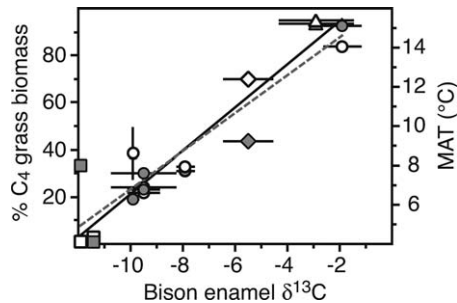


Figure 2. Mean $\delta^{13}\text{C}$ of enamel plotted against measured percentage of C_4 grass (open symbols) and mean annual temperature (MAT) (gray symbols). X-axis error bars represent one standard deviation (1σ) of enamel $\delta^{13}\text{C}$ values. Y-axis error bars represent the range of measured C_4 abundances. Solid line—regression line through the data; dashed line—theoretical line of perfect fit (slope = 1); circles—mixed-grass prairie; triangles—tallgrass prairie; diamonds—sandhills prairie; squares—mountain grasslands.

Harris, 1999). Thus, the values of older museum samples (collected 1905–1948) were corrected for this effect (Marino and McElroy, 1991), and corrected values were used in data analyses (Table DR2; see footnote 1). The mean $\delta^{13}\text{C}$ values for the bison populations analyzed vary by 10‰ and reflect geographic variation in the abundance of C_4 grasses (Table DR1, see footnote 1; Fig. 2). The variance of bison populations is similar to the variance of terrestrial herbivores reported by Clementz and Koch (2001) (F test, $p > .05$), who demonstrated that at least five animals must be measured to accurately estimate population mean $\delta^{13}\text{C}$ values and standard deviation (i.e., mean standard error $\leq 0.01\%$). Thus, bison populations with fewer than five individuals (National Bison Range and Yellowstone) were excluded from comparisons of variability. The remaining populations displayed no significant differences in variability (F test, $p \geq .1$), and difference in variability did not correlate with the abundance of C_4 grasses ($r = .49$, $p = .27$), mean annual temperature (MAT) ($r = .44$, $p = .32$), mean annual precipitation (MAP) ($r = .66$, $p = .11$), range size ($r = .34$, $p = .46$), or sample size ($r = .12$, $p = .80$).

Mean enamel $\delta^{13}\text{C}$ values are strongly correlated with the abundance of C_4 grasses ($r = .97$, $p < .0001$). Therefore, least-squares regression of the $\delta^{13}\text{C}$ values of enamel against the local abundance of C_4 grasses can be used to predict the abundance of C_4 grasses:

$$\begin{aligned} \% \text{C}_4 = & [9.16(\pm 0.94) \\ & \times \text{mean } \delta^{13}\text{C}_{\text{Enamel}}] \\ & + 112.80(\pm 0.80) \\ & (r = .97, p < .001). \end{aligned} \quad (1)$$

The intercept and slope of the line are reported \pm the standard error. Exclusion of the two sites with low numbers of bison does not significantly change equation 1, which demonstrates that the relationship between the $\delta^{13}\text{C}$ of enamel and the abundance of C_4 grasses is robust.

DISCUSSION

Although mean enamel $\delta^{13}\text{C}$ values correlate with measured C_4 abundances, bison within the same population display $\delta^{13}\text{C}$ values that vary $\leq 3\text{‰}$ (Table DR1; see footnote 1). Several factors may cause this variability: (1) Bison from the same population often feed in different habitats, and thus can consume diets that vary seasonally by $> 1\text{‰}$ owing to habitat-level variations in C_4 abundance (Coppedge and Shaw, 1998; Coppedge et al., 1998; Post et al., 2001) and variations in the $\delta^{13}\text{C}$ of plants caused by changes in local environmental conditions, such as degree of water stress (Farquhar et al., 1989); (2) because the abundance of C_4 grasses varies annually with changes in temperature and precipitation (Tieszen, 1998), teeth that mineralized in different years can display different $\delta^{13}\text{C}$ values; (3) because C_4 abundance varies seasonally (Tieszen and Boutton, 1989), enamel samples that represent either more or less than exactly 1 yr of growth will be offset from mean annual values.

Such sampling errors should be minimized in this study because samples were collected from only the third molar, and sample size was standardized to represent material mineralized over 1 yr of growth. However, the observed variability of enamel $\delta^{13}\text{C}$ values emphasizes the importance of using the mean values of multiple bison for paleoenvironmental reconstructions. Because bones are continually remodeled through life, they may display less intrapopulation $\delta^{13}\text{C}$ variability than enamel (see Tieszen et al., 1988). Thus, $\delta^{13}\text{C}$ analyses of bones from fewer individuals may provide a good estimate of population mean, but tooth enamel is more resistant to postmortem alteration and thus more likely to preserve biogenic $\delta^{13}\text{C}$ values in most fossils.

The strong correlation between enamel $\delta^{13}\text{C}$ values and the measured abundance of C_4 grasses (Eq. 1) demonstrates that mean bison enamel $\delta^{13}\text{C}$ values can be used as a quantitative proxy for reconstructing the relative abundance of C_4 grasses. The percentage of C_4 plants in bison diets can be calculated using the diet-enamel fractionation of $14.6 \pm 0.3\text{‰}$ as determined by Passey et al., (2005).² The regression of calculated dietary C_4 abun-

²The percentage of C_4 in diet is calculated using the equation: $\delta^{13}\text{C}_{\text{enamel}} = [\delta^{13}\text{C}_{\text{Pure C}_4 \text{ feeder}} \times (X)] + [\delta^{13}\text{C}_{\text{Pure C}_3 \text{ feeder}} \times (1 - X)]$, where X = dietary percentage of C_4 plants (Koch et al., 1998).

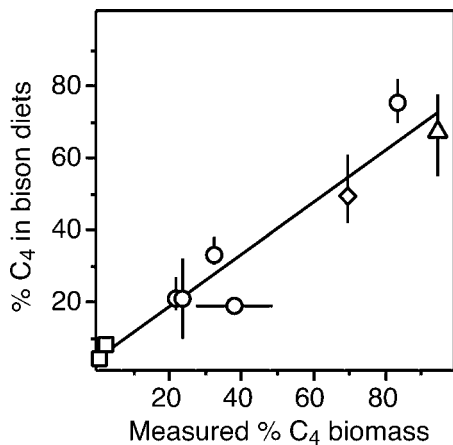


Figure 3. Calculated mean percentage of C_4 abundance in bison diets plotted against measured percentage of C_4 biomass. Error bars represent the range of values at each site. Symbols defined in Figure 2.

dance against the measured grassland C_4 abundance (Fig. 3) yields the equation:

$$\begin{aligned} \text{Mean \%C}_4(\text{diet}) &= [0.72(\pm 0.07) \\ &\times \text{measured \%C}_4] \\ &+ 3.02(\pm 3.85) \\ (r &= .97, p < .001). \quad (2) \end{aligned}$$

Calculated dietary C_4 abundances differ $<5\%$ from measured C_4 abundance at areas dominated by C_3 grasses. However, in areas dominated by C_4 grasses (i.e., $\%C_4 \geq 70\%$), calculated dietary C_4 abundance underestimates the C_4 abundances by 10% to $\sim 27\%$. This difference is most likely caused by selective feeding by bison, which have been observed to preferentially feed on protein-rich C_3 grasses in mixed C_3/C_4 grasslands on a seasonal basis (Tieszen, 1998). Calculated diets are within 10% of previous reconstructions of dietary C_4 grass abundance on the basis of microhistological and/or isotopic analyses of feces for all populations that have been studied (Yellowstone, Wind Cave, Fort Niobrara, and Tallgrass Prairie) (Iowa Cooperative Wildlife Research Unit, 1981; Coppedge and Shaw, 1998; Tieszen, 1998; Feranec, 2004). This suggests that mean enamel $\delta^{13}\text{C}$ values accurately estimate dietary abundance of C_4 grasses. Using equation 1 to calculate C_4 abundances yields estimated C_4 abundances that average within 10% of the measured values for all sites, including those dominated by C_4 grasses.

Previous research on Great Plains grasslands has demonstrated that, overall, 78% of the variability in the percentage contribution of C_4 grasses to total grass biomass can be explained by MAT (66%), MAP (5%), and local soil textures (7%) (Epstein et al., 1997),

although grasses in the Sandhills Prairie, which has sandy, well-drained soils, are more strongly influenced by the amount and timing of growing season precipitation (Yang et al., 1998) than vegetation in other areas. Because bison $\delta^{13}\text{C}$ values closely mirror local C_4 grass abundance, they should also serve as a proxy for reconstructing paleoclimatic conditions, particularly paleotemperatures. We can test this hypothesis by regressing mean bison $\delta^{13}\text{C}$ values against MAT (National Oceanic and Atmospheric Administration, 2003), which yields a significant correlation ($r = .91$, $p < .001$). Thus, MAT can be calculated from enamel $\delta^{13}\text{C}$ values (Fig. 2) using the equation:

$$\begin{aligned} \text{MAT} &= [0.97(\pm 0.16) \\ &\times \text{mean } \delta^{13}\text{C}_{\text{Enamel}}] \\ &+ 16.44(\pm 1.39) \\ (r &= .91, p < .001). \quad (3) \end{aligned}$$

This relationship does not display a significant departure from linearity ($p = .50$), but additional data points from locations with MAT between 9 and 15 °C are needed to confirm whether this pattern is robust. Multiple regression analysis of mean enamel $\delta^{13}\text{C}$ values with respect to MAT and MAP did not yield a significant correlation between $\delta^{13}\text{C}$ and MAP, confirming that MAP does not contribute greatly to the variability in bison $\delta^{13}\text{C}$ values. This is not surprising, given the relatively low contribution of modern MAP ($\sim 5\%$) to overall C_4 variability (Epstein et al., 1997). The correlation for bison $\delta^{13}\text{C}$ values and MAT is better than that for measured C_4 abundance and MAT. This suggests that bison may homogenize local geographic and temporal variation in C_4 abundance better than current vegetation sampling techniques. Overall, the correlation between bison $\delta^{13}\text{C}$ values and MAT suggests that the $\delta^{13}\text{C}$ of bison can be used as a proxy for reconstructing paleotemperatures. However, several factors must first be accounted for: (1) Changes in soil texture can affect the local abundance of C_4 grasses; e.g., the $\delta^{13}\text{C}$ of bison from the sandhills prairie and mountain grasslands deviate from the regression line (Fig. 2), whereas regression of the $\delta^{13}\text{C}$ values of bison from similar habitats in the Great Plains (mixed-grass and tallgrass prairie) against MAT yields an equation that is statistically identical to equation 3 with $r = .99$. This emphasizes the importance of accounting for changes in soil texture and vegetation habitat when using bison $\delta^{13}\text{C}$ values to reconstruct MAT. (2) Changes in the $\delta^{13}\text{C}$ of atmospheric CO_2 must be accounted for (e.g., Marino and McElroy, 1991). (3) The effects of lower $p\text{CO}_2$ levels must be accounted for because C_3/C_4 ratios will decrease with de-

creasing $p\text{CO}_2$ levels, and reconstructed MAT will reflect minimum values (Ehleringer et al., 1997). (4) Finally, we must establish whether the diets and migration patterns of fossil bison differed from those of modern animals.

Isotopic evidence suggests that fossil bison had diets similar to their modern counterparts. The $\delta^{13}\text{C}$ of Pleistocene bison from Texas and the southwestern United States shows that the bison consumed 80%–90% C_4 grass in C_4 dominated ecosystems (Connin et al., 1998; Koch et al., 2004). Reconstructions of the migratory habits of prehistoric bison have yielded mixed results. The $\delta^{13}\text{C}$ of bone collagen suggests that in Canada some bison migrated distances of a few hundred kilometers, whereas others ranged only locally (Chisholm et al., 1986). In contrast, enamel $\delta^{13}\text{C}$ values of bison from Texas displayed low variability ($1\sigma \leq 1.2\text{‰}$) similar to that of modern animals, suggesting that Texas bison ranged only locally. Corresponding analyses of oxygen isotope ratios likewise suggest that these bison were not migratory (Koch et al., 2004; Hoppe, 2006). These results suggest that bison may have displayed different migratory behavior in different regions. Thus, it is important to reconstruct geographic variations in bison migration patterns. Isotopic analyses of serial samples of accreted tissues (e.g., hair, horn, or tooth enamel) may provide detailed information about the migration patterns, and analyses of bulk enamel $\delta^{13}\text{C}$ values in combination with other isotopic signals, such as oxygen and strontium isotope ratios, should help in distinguishing between resident and migratory individuals (e.g., Hoppe, 2004).

A test of the accuracy of paleotemperature calculations can be conducted using analyses of fossil bison ($n = 5$) from Friesenhahn Cave, Texas, ranging in age from 17,800 to 19,600 radiocarbon yr B.P. and yielding a mean $\delta^{13}\text{C}$ value of $1.5\text{‰} \pm 1.2$ (Koch et al., 2004). Once these $\delta^{13}\text{C}$ values are corrected for the 0.9‰ shift in the $\delta^{13}\text{C}$ of atmospheric CO_2 , equation 3 can be used to calculate that MAT was 14.1 °C, which is within 2 °C of modeled MAT for this location during this time period (see discussion in Koch et al., 2004). However, analyses of multiple bison from areas with different paleoclimates and vegetation patterns need to be conducted and compared with regional paleoclimatic models in order to fully assess the accuracy of temperature estimates.

CONCLUSIONS

Our analysis shows that bison $\delta^{13}\text{C}$ values can be used to quantify grassland C_3/C_4 ratios across different ecosystems. Mean $\delta^{13}\text{C}$ values of tooth enamel from bison can be used to quantify the abundance of C_4 grass biomass to within $\pm 10\%$, and thus analyses of $\delta^{13}\text{C}$ values from fossil bison have good potential

for use as a quantitative proxy for reconstructing C₄ abundance in ancient grasslands. In addition, because C₃/C₄ ratios correlate with MAT, analyses of bison δ¹³C values can also provide information about paleotemperatures, although the influence of possible changes in soil type and atmospheric CO₂ must be accounted for to quantify paleotemperature precisely. Furthermore, spatial integration of local environmental signals may result from the inclusion of migratory bison in paleoenvironmental reconstructions. Thus, analyses of other isotopic systems should be used to identify potential migrants. Given the complex interactions between these environmental and biological factors, it seems likely that the δ¹³C values of fossil bison will best serve as a qualitative measure of paleotemperature or for quantitatively estimating temperature gradients among sites that were deposited at the same time. Despite these complications, our results demonstrate that analyses of the δ¹³C of fossil bison can provide valuable information about paleovegetation gradients and paleoclimatic conditions.

ACKNOWLEDGMENTS

The following people helped collect and interpret data: C. Conroy, G. Fredlund, B. Hamilton, A. Hoppe, R. Huber, B. Kenner, C. Kimball, K.J. Kimball, P. Koch, J. Mason, M. Mellott, M. Miller, B. Muenchau, M. Oehler, B. Peterson, J. Street, and J. Waldbauer. D. Fox and L. Tieszen provided manuscript reviews. A U.S. National Science Foundation ADVANCE Fellows grant to K. Hoppe provided funding.

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Manuscript received 20 February 2006

Revised manuscript received 15 March 2006

Manuscript accepted 17 March 2006

Printed in USA