Residual amino acid fluxes in the upper water column of the Bransfield Strait

Drifting sediment traps
Bransfield Strait
Amino acid fluxes

Pièges à sédiments dérivants
Détroit de Bransfield
Flux d'acides aminés

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ABSTRACT

Fluxes of residual amino acids were determined on samples from two drifting sediment traps deployed at 100 m water depth in the Bransfield Strait in December 1980. Differences in the absolute fluxes were related to the sources of sedimenting particulate matter. The relative contributions of amino acids to the total flux and the molar composition were similar for both traps.
Comparison with published particulate amino acid fluxes indicates that a distinction must be made between high and low production environments. In the former case, 90% of the primary amino acid production is degraded within the upper 100 metres of the water column, whereas in the latter case this zone is extended to approximately 1,000 m.

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RÉSUMÉ

Flux d'acides aminés résiduels dans la colonne d'eau supérieure du détroit de Bransfield

Les flux d'acides aminés résiduels ont été estimés sur des échantillons issus de pièces à sédiments dérivants, déployés à 100 m de profondeur dans le détroit de Bransfield en décembre 1980. Les différences observées dans les flux absolus sont reliées aux sources du matériel particulaire sédimenté. La contribution relative et la composition molaire des acides aminés participant au flux total sont identiques d'un piège à l'autre.
La comparaison des flux entre nos résultats et ceux de la littérature indique qu'une distinction doit être faite entre des milieux à forte et à faible production. Dans le premier cas, 90% de la production d'acides aminés sont dégradés dans les 100 premiers mètres de la colonne d'eau; tandis que dans l'autre cas, cette couche peut atteindre environ 1 000 m.

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INTRODUCTION

Although most planktonic primary production is recycled within the upper few hundred metres of the water column (Eppley, Peterson, 1979), the remaining particulate organic matter, transported to deeper water layers and/or the sea bottom, represents an important food source for deep-sea heterotrophs. It is now generally accepted that most of this flux is in the form of large particles (> 200 µm) such as faecal pellets and marine snow (Suess, 1980).

Whereas a wealth of data is available for bulk properties of this particle flux, concerning for example total organic carbon or nitrogen contents, little is known about the contributions of individual compounds to the flux. Lipids (Prahl, Carpenter, 1979; Tanoue, Handa, 1980; Wakeham *et al.*, 1980; De Baar *et al.*, 1983; Lee *et al.*, 1983), amino acids (Wakeham *et al.*, 1980 ; Lee, Cronin, 1982; Wefer *et al.*, 1982; Lee *et al.*, 1983) and carbohydrates

(Wefer *et al.*, 1982) have been reported as constituents of the total organic carbon pool.

More data are, however, required to understand and to model processes affecting the transport of individual compounds from the zone of production to deeper parts of the water column and the sediment surface. In the present communication, amino acid fluxes from the Bransfield Strait measured during the Antarctic phytoplankton spring bloom are presented and discussed in relation to plankton composition.

MATERIAL AND METHODS

Drifting sediment traps were deployed in December 1980 in the Bransfield Strait (Fig. 1). Background data are listed in Table 1. The design of the traps employed has been described by Zeitschel *et al.* (1978). Details of the drifting buoy system used may be found in the report of Petersohn *et al.* (1981).

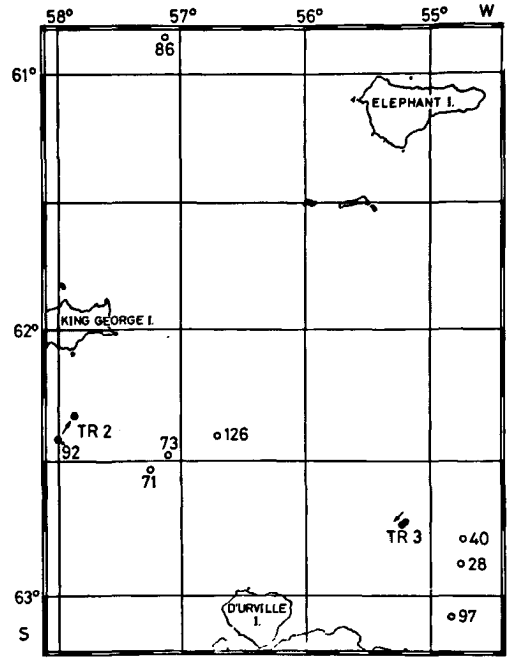

Figure 1
Location of sediment traps and hydrostations in the Bransfield Strait.

After recovery, the particulate material was manually homogenized in 250 cm^3 of filter-sterilized seawater and 5 cm^3 aliquots were filtered through precombusted (450°C, overnight) GF/C filters. Water column particulate material was obtained from 10 dm^3 Niskin samplers (General Oceanic Inc.). Depending on the particulate load, 0.5 to 2 dm^3 water was filtered through precombusted GF/C filters. All filters were stored deep frozen until final analysis.

After thawing, the filters were extracted with chloroform/methanol 2:1 followed by a hot water extraction as described by Schumann (1983). The remaining particulate material was then subjected to hydrolysis with 6M HCl at 110°C for 24 hours under nitrogen. After centrifugation, an aliquot was analysed for amino acids by the high performance liquid chromatographic technique of Lindroth and Mopper (1979). Quantification was by comparison with an external standard using α-amino butyric acid as internal standard as described by Dawson and Liebezeit (1983).

Table 1
Background data for free drifting sediment traps TR2 and TR3.

Trap	Deployment time	Deployment depth	Euphotic zone depth	Catchment area
	[h]	[m]	[m]	[cm^2]
TR2	03. -05.12. 23.00-06.00 h	30	100	20	314
TR3	07. -08.12. 12.00-12.00 h	24	100	100	314

Due to the extraction procedure employed before hydrolysis, only amino acids not soluble in chloroform/methanol, such as *e.g.* lipoproteins, or in water, such as *e.g.* intracellular free amino acids, will be determined with the procedure used here. These will be referred to in the following as residual amino acids.

Schumann (1983) employing the same technique found that 70-80% of the total amino acids were residual. Lee and Cronin (1982) reported that on the average 7.4% of the total hydrolysable amino acids were extracted with toluene/methanol 1:1. The hot water extraction of Bölter and Dawson (1982) yielded a mean of 16.1% of the total amino acids present.

From the above figures it is obvious that the terms extractable and residual are operationally defined. For the calculations of the present paper, it will be assumed that residual amico acids account for 75% of the total.

RESULTS AND DISCUSSION

Preliminary analysis of phytoplankton composition in the Bransfield Strait in December 1980 indicated that the northern part extending towards the eastern exit was dominated by a dense bloom of *Phaeocystis* sp. (von Bodungen *et al.*, 1981; Elbrächter, 1981). The high biomass values found here are reflected in high chlorophyll contents (5-11 μg dm^{-3}; von Bodungen *et al.*, 1981; Haardt, Maaßen, 1983), high particulate carbohydrate contents (600 nmoles dm^{-3}; Liebezeit, 1984) and a compressed euphotic zone of around 20 m (von Bodungen, pers. comm., 1983). Beneath the *Phaeocystis* layer, diatoms were found in bad physiological conditions (von Bodungen, pers. comm., 1983).

In the southern part of the Bransfield Strait, towards the ice edge, bacillariophyceae were dominant. The species composition here was similar to that of the diatoms found underneath the *Phaeocystis* zone (von

Bodungen, pers. comm., 1983). Here, chlorophyll values ranged from 1-5 µg dm^{-3}, von Bodungen *et al.*, 1981; Haardt, Maaßen, 1983) in an extended euphotic zone of around 100 m (von Bodungen, pers. comm., 1983). Particulate carbohydrates were found to be around 200 nmoles dm^{-3} with a predominance of glucose, whereas a more homogenous distribution was found in the northern part (Liebezeit, 1984).

These two zones will be referred to in the following as *Phaeocystis* and diatom zones respectively.

TR 2, deployed in the *Phaoecystis* zone, showed mean fluxes of 32.8 mg amino acid carbon and 10.1 mg amino acid nitrogen m^{-2} d^{-1} corresponding to 23.8 and 52.6% of the total carbon and nitrogen fluxes, respectively (Fig. 2). Since primary production measurements are generally expressed in terms of carbon in the following amino acid carbon values will be discussed preferentially.

The major contribution to the carbon flux was from glutamic acid (Fig. 2). Isoleucine, leucine, phenylalanine, aspartic acid and histidine each contributed around 8%, whereas all other acids accounted for less than 5 % of the amino acid flux. The non-protein acids ß-alanine, citrulline, α-amino butyric acid and ornithine were either absent or present in trace amounts only, indicating a minor contribution from bacterial sources (Lee, Cronin, 1982).

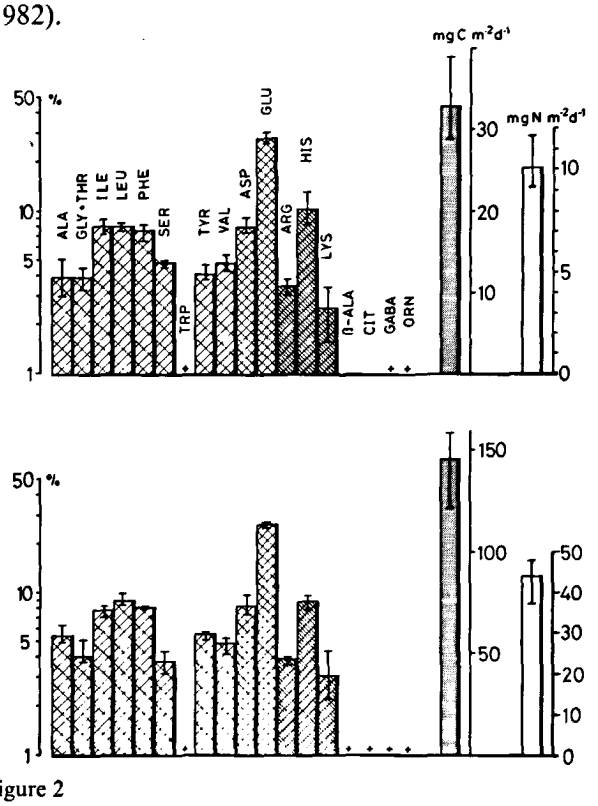

Figure 2

Total amino acid carbon and nitrogen fluxes and relative contributions of individual amino acids to the total carbon flux for TR 2 (upper part) and TR 3 (lower part). Abbreviations: ALA = alanine, GLY = glycine, THR = threonine, ILE = isoleucine, LEU = leucine, PHE = phenylalanine, SER = serine, TRP = tryptophan, TYR = tyrosine, VAL = valine, ASP = aspartic acid, GLU = glutamic acid, ARG = arginine, HIS = histidine, LYS = lysine, ß-ALA = ß-alanine, CIT = citrulline, GABA = γ-amino butyric acid, ORN = ornithine. + denotes a contribution of less than 1%.

TR 3 deployed in the diatom zone, showed considerably higher fluxes (Fig. 2) these being 145.5 mg amino acid carbon and 44.3 mg amino acid nitrogen m^{-2} d^{-1}. The relative contributions to the total fluxes (25.3 and 49.6%) were, however, similar to those of TR 2. The contributions of the individual amino acids to the total flux were also similar to those of TR 2, and statistical analysis of both data sets (TR 2 vs TR 3; Tab. 2) resulted in a highly significant linear correlation (r = 0.9892).

Table 2

Mean molar composition of particulate material.

	Sediment traps		Stations	
	TR2	TR3	92 (0-40 m)	97 (0-100 m)
n*	3	4	5	6
ALA	6.4	8.9	6.1	7.6
GLY	9.8	10.3	8.0	10.4
ILE	6.7	6.4	6.4	6.1
LEU	6.7	7.2	7.8	6.1
PHE	4.2	4.4	4.5	3.6
SER	7.9	6.1	6.3	6.3
TRP	0.1	–	–	0.1
TYR	2.3	3.0	2.7	2.6
VAL	4.7	4.7	5.1	4.3
ASP	10.0	10.1	12.0	9.9
GLU	27.4	25.7	27.6	30.4
ARG	2.8	3.1	3.7	2.8
HIS	8.5	7.2	7.4	6.8
LYS	2.1	2.5	2.0	2.3
ß-ALA	–	0.1	–	0.1
γ-ABA	0.1	0.2	0.1	0.1
ORN	0.4	0.3	0.3	0.6
$\bar{x}$**	563	2.497	1.340	0.927
Range**	497-666	2.092-2.714	0.846-2.104	0.822-1.067

* Number of replicates (TR2 and TR3) or samples from the euphotic zone (stations 92 and 97)

** Mean values and ranges in [µmoles m^{-2} d^{-1}] for TR2 and TR3 and [µmoles dm^{-3}] for stations 92 and 97.

– Denotes contents < 0.1 mol%.

The amino acid C/N ratios of 3.25 and 3.28 compare well with those found by Lee and Cronin (1982) for the Peru upwelling area of 3.56 and calculated by Jukes *et al.* (1975) for an average protein of 3.06.

Microscopic examination of the trap contents showed TR 2 to contain mostly zooplankton faecal pellets, presumably derived from krill (*Euphasia superba*/von Bodungen *et al.*, 1981).

Cowey and Corner (1966) and Tanoue *et al.* (1982) demonstrated for *Calanus finmarchicus* and *E. superba*, respectively, that the molar composition of the amino acids in faecal pellets of these species is not significantly different from that of their food. Tanoue *et al.* (1982) furthermore established the importance of amino acids in the nutrition of krill.

The amino acid contribution to the total carbon pool in krill faecal pellets decreases by 35% (Tanoue *et al.*, 1982) compared to the food, whereas the amino acid flux for TR 2 is 77% less than that for TR 3 (Fig. 2). Thus, the discrepancy between amino acid fluxes in both traps can only be partially

explained by conversion of living phytoplankton into zooplankton faecal pellets.

It is at present unclear whether *E. superba* feeds on *Phaeocystis* or on the diatoms found underneath this layer. Statistical analysis of residual amino acids from station 92 (*Phaeocystis* zone; Fig. 1) and station 97 (diatom zone; Fig. 1) indicates that a highly significant linear correlation exists between samples from the euphotic zones of both stations (Tab. 2; r = 0.9860), and thus no further conclusions can be drawn on the basis of the amino acid data.

Particulate carbohydrates at station 137 in the western part of the Bransfield Strait, also dominated by *Phaeocystis*, show a rapid decrease from 600 nmoles dm^{-3} in the upper 20 m to 90 nmoles dm^{-3} at 100 m depth (Liebezeit, 1984). This has been linked with a rapid degradation of *Phaeocystis* colonies sinking out of the euphotic zone. A similar effect has been observed for residual amino acids at station 73 (Fig. 1) where a decrease from 1,287 to 183 nmoles dm^{-3} occurred from the surface to 100 m depth (Liebezeit, Bölter, in prep.).

Lee and Cronin (1982) found 78% of the amino acids produced in the euphotic zone to be lost at the base of this layer and concluded that most of these "lost" amino acids had been transferred to the dissolved pool. Bölter and Dawson (1982) reported a striking similarity in the spectra of dissolved combined and particulate combined amino acids for stations 68 and 73 (Fig. 1). This points to a degradative mechanism in Antarctic waters similar to that discussed by Lee and Cronin (1982) for the Peru upwelling.

TR 3 contents were mainly found to be diatom chains (von Bodungen *et al.*, 1981). Although the residual amino acids in diatom dominated waters were found to be only half of those found in the *Phaeocystis* zone (Tab. 2), the depth distribution was homogenous for the upper 100 m: *e.g.* at station 97 (Fig. 1) a slight increase from 865 nmoles dm^{-3} at the surface to 1,065 nmoles dm^{-3} at 100 m depth was found (Liebezeit, Bölter, in prep.).

Assuming a homogenous distribution of particulate matter in the water column, the flux of 2,496 µmoles m^{-2} d^{-1} would be equivalent to a water column of 2.7 m (range 2.3 – 3.1 m) using 927 µmoles m^{-3} (range 819 – 1,067 µmoles m^{-3}) as an average value for station 97. From total particulate phosphorus fluxes, von Bodungen *et al.* (1981) calculated a similar value of 3 m water column.

The high statistical correlation between both trap samples and water column particulates is noteworthy. The four data sets of Table 2 are all correlated at the 99.9% confidence level. Whether this reflects an adaptation of the pool of residual amino acids to the cold environment cannot be positively established at the moment, and additional data from *e.g.* pure cultures are needed to confirm this hypothesis. Particulate carbohydrate analyses from both water column particulate matter (Liebezeit, 1984) and trap samples (Liebezeit, unpublished results) show, however, distinct differences between the *Phaeocystis* and diatom zones and thus support the above adaptation hypothesis.

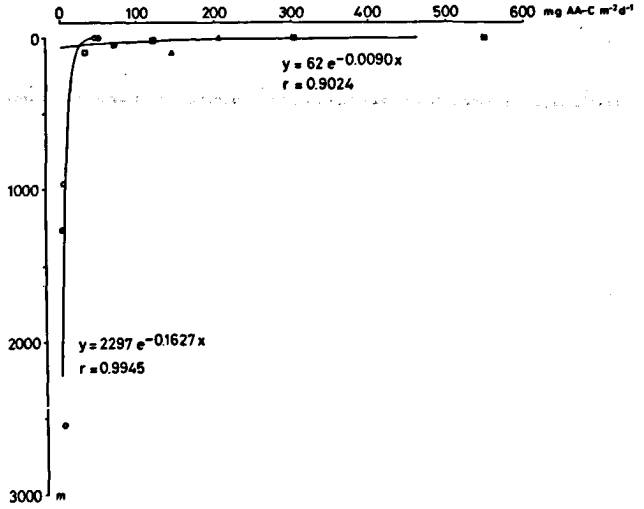

Figure 3

Relationship between amino acid production and flux, respectively, and water depth. Data for Peru upwelling (filled squares) from Lee and Cronin (1982), Drake Passage (circles) from Wefer et al., *(1982) and Panama Basin (dots) from Lee* et al. *(1983). TR 2 (squares) and TR 3 (triangles). TR 3 data were not used for calculation of exponential regression.*

Suess (1980) has compiled carbon flux data from different parts and depths of the world oceans and found a non-linear decrease with depth. His results have recently been corroborated by Lorenzen *et al.* (1983). An approach similar to that of Suess (1980) can be made for amino acid fluxes using the results of this study and published fluxes (Fig. 3).

In highly productive environments such as the Peru upwelling or the *Phaeocystis* zone of this study with high grazing pressure a rapid decrease is to be observed in the upper water column. For TR 2, an amino acid production within the euphotic zone of 302.5 mg amino acid carbon m^2 d^{-1} can be calculated using a mean total primary production of 1,210 mg C m^{-2} d^{-1} (mean value from stations 71, 92 and 126; Tilzer, von Bodungen, 1981) and assuming as a conservative estimate that 25 % of this carbon is in the form of amino acids (Lee, Cronin, 1982). At 100 m the flux of 32.8 mg amino acid carbon m^{-2} d^{-1} corresponds to 10.8% of the euphotic zone production. This figure compares well with the 11.4% of the total particulate organic carbon remaining at this depth (von Bodungen, pers. comm., 1983). The corresponding values reported by Lee and Cronin (1982) are 22% at the base of the euphotic zone and 12% at 50 m.

A second type of high production environment is represented by the TR 3 samples. Primary production in the euphotic zone is about 30% lower here than in the *Phaeocystis* zone. Thus, from a mean total production of 825 mg C m^{-2} d^{-1} (stations 28 and 40; Fig. 1; Tilzer, von Bodungen, 1981), an amino acid production of 206 mg amino acid carbon m^{-2} d^{-1} is calculated. The 100 m flux of 145.5 mg

amino acid carbon m^{-2} d^{-1} corresponds to 70.6% of the euphotic zone production. Similarly, von Bodungen (pers. comm., 1983) found a 31% reduction in total carbon at this depth. This suggests that in both cases the degradation of the bulk of particulate organic carbon and amino acids proceeds at a similar rate.

Since there is no evidence from planktological observations of zooplankton grazing in the diatom zone, it can be assumed that a much higher percentage of both particulate amino acids and carbon will reach deeper water layers. This is supported by findings of Billett *et al.* (1983), who reported on the presence of intact diatom chains at water depths from 1,370 to 4,100 m in the northeast Atlantic as a result of the sinking of a phytoplankton bloom. The presence of a complex mixture of carotenoids and chlorophylls indicated that these had reached the sea bottom virtually unchanged, although the total content of chloropigments decreased by two orders of magnitude with increasing water depth, hinting at the activity of deep sea heterotrophs.

A third type is represented by the open ocean environment studied by Wefer *et al.* (1982). Although the phytoplankton at their site close to station 86 (Fig. 1) was dominated by bacillariophyceae as well (von Bodungen *et al.*, 1981) total primary productivity was considerably lower than in the Bransfield Strait (100 mg C m^{-2} d^{-1}; Tilzer, von Bodungen, 1981). The 44.9 mg amino acid carbon m^{-2} d^{-1} reported by Wefer *et al.* (1982) corresponding to 44.9% of the total produced are higher than the 25% reported by Lee and Cronin (1982) and used here. The mean value of 27 samples analysed for residual amino acids from the euphotic zone of the diatom zone were found to be 22.9 ± 7.3% of the total particulate organic carbon. Assuming that this represents 75% of the total amino acids (*see* above) it seems justified to use the value of 25% as a conservative figure. It should, however, be pointed out that the 44.9% of Wefer *et al.* (1982) are the result of a single measurement. Liebezeit and Bölter (in prep.) found residual amino acids to contribute 13.1 – 47.0% of the total particulate organic carbon in samples from the Bransfield Strait.

Analysis of the data of Lee and Cronin (1982), Wefer *et al.* (1982), Lee *et al.* (1983) and the results of this study suggest (Fig. 3) that a distinction has to be made between high and low productivity environments. In the former, where a considerable grazing pressure can be expected, amino acids are rapidly degraded within the upper water layers (Peru upwelling, TR 2). Where such a pressure does not exist, as in the case of the TR 3 location, a high proportion of the originally produced organic matter will reach deeper water layers and/or the sea bottom. It should, however, be pointed out that these high production environments are generally coastal in nature and that the role of sediment resuspension in shallow waters (*e.g.* Tsunogai *et al.*, 1980) or chemoautotrophic activity at the sediment surface (Lee, Cronin, 1982) cannot be assessed at present. From the data available so far it seems that approximately 10% of the primary production will reach the sediment here.

Open ocean environments with low primary productivity, on the other hand, show a considerably slower degradation rate, thus extending the zone where 90% of the primary production is degraded to approximately one thousand metres (Fig. 3).

Gardner *et al.* (1983), measuring decay rates of particulate organic matter inside and outside sedimenty traps at different depths, arrived at losses of 0.1 – 1% of organic carbon/day. Schumann (1983), while studying the effects of chloroform as fixing agent on the amino acid composition of particulate matter, reported an average loss of 6.3% over a 2 days period with individual amino acids showing losses of 3.5 to 20.0% compared to the original sample. This rate is higher than those reported by Gardner *et al.*, (1983) but, as pointed out by these authors, the degradation rates may decrease exponentially and averaging over a longer time span will result in lower decay rates.

From the presence of muramic acid in their samples Lee *et al.* (1983) concluded that bacterial colonization of sediment trap material had occurred despite the fact that sodium azide had been used as poisoning agent.

These findings may have no serious consequences for the sediment trap data from the Bransfield Strait discussed here, due to the short deployment times. Longer collecting periods, as in the case of the Drake Passage or the Panama Basin samples, may, however, result in changes both in the absolute amino acid fluxes and the relative composition of the amino acid fluxes and the relative composition of the amino acid pools. But these processes are difficult to quantify, and further work is needed to establish the effects of: a) leaching of water-soluble compounds during deployment; b) autolysis of sedimented phytoplankton; and c) bacterial degradation and *de novo* synthesis of particulate organic matter.

Amino acids in the upper 1,000 m of the water column contribute on the average 24% of the total particulate organic carbon flux (Fig. 4), indicating that these compounds are degraded at a rate similar to that of the bulk of carbon. Towards greater depths, a decrease in this contribution is to be observed. However, the data of Lee *et al.* (1983) from the Panama Basin (Fig. 4) indicate a high variability of this relative proportion thus stressing the need for further analyses.

The contribution of amino acids to the total organic nitrogen pool show a greater variability but do not seem to change significantly with depth (Fig. 4).

From experiments of Newell (1965) it can, however, be inferred that this is not necessarily due to a non-degradation of proteinaceous material. Microbial colonization of particles and hence *de novo* production of organic material may also be responsible for the more or less constant contributions of

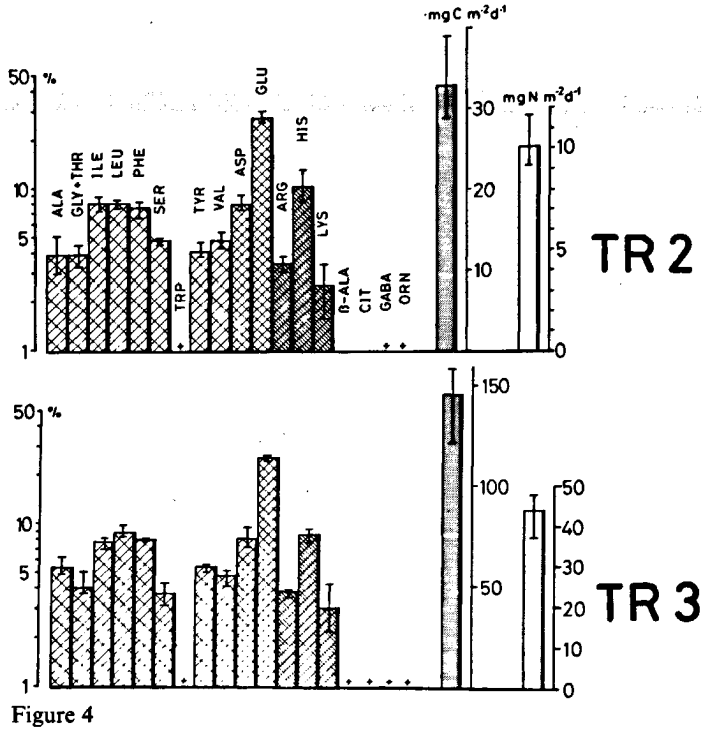

Figure 4

Relative contributions of amino acids to the total organic carbon and nitrogen fluxes. Data from Wefer et al. *(1982; M 269), Lee and Cronin (1982; PU [Peru upwelling]) and Lee* et al. *(1983; PB [Panama Basin]).*

particulate amino acids to both the total carbon and nitrogen pools.

From the discussion above, it should be clear that the conclusions drawn can only be tentative at present, and that further experimentation is needed to support the hypotheses outlined.

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