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ESTIMATING CROP RESIDUE DECOMPOSITION COEFFICIENTS USING SUBSTRATE-INDUCED RESPIRATION

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Summary—Modeling of crop residue decomposition for nutrient cycling and effectiveness of residues to control soil erosion requires information on crop-specific decomposition coefficients (k). Respiration of decomposing residues reflects the activity of the microbial community and should give an indication of the residue decomposition rate. A method for estimating k using substrate-induced respiration (SIR) of plant residues was evaluated. Basal respiration, total SIR, fungal SIR and bacterial SIR were measured for five crop residues monthly for 1 y. In general, total SIR and basal respiration declined for the more decomposable residues, but were somewhat constant for the more resistant residues. Mass loss was used to determine k for a single exponential decay function. Prediction of k from SIR using an equation proposed by Neely *et al.* (1991) (*Soil Biology & Biochemistry* **23**, 947–954) was unsatisfactory for the five crops. A new equation ($k = -6.07 \times 10^{-4} + 6.23 \times 10^{-6} \times \text{SIR}$) was determined using the data of Neely *et al.* (1991) and data from the current study. Prediction of k using the 60-day SIR measurement was significantly improved with the new equation. Predicting k from SIR could greatly reduce the labor and time involved in evaluating decomposition differences between residues and locations. Published by Elsevier Science Ltd

INTRODUCTION

Crop residue management practices influence agricultural sustainability by altering the rate of organic matter addition, soil physical and chemical properties, and soil temperature and water regimes, which all interact with microbial activity and diversity (Doran and Smith, 1987). Microbial communities are responsive to shifts in residue resource quality and environment (Beare *et al.*, 1992). Those organisms capable of rapid growth have an advantage during early stages of residue decomposition, whereas organisms capable of producing enzymes that degrade complex organic molecules are favored during later stages (Stott and Martin, 1989). Microbial community size and diversity in general must reflect resource availability and quality.

The role of microorganisms in nutrient cycling and energy processes of soil ecosystems has been measured by many methods (Wardle, 1992). Substrate-induced respiration (SIR) was developed to measure the response of the 'metabolically active' component of the microbial community (Anderson and Domsch, 1978) and has been adapted for use in dry and wet soil (West and Sparling, 1986) and plant residues (Beare *et al.*, 1990, 1991). Substrate-induced respiration reflects the size of the active microbial biomass since it evaluates the maximum potential activity, not the actual activity, occurring for the residue at the time of sampling. Beare *et al.* (1990, 1991) observed a strong correlation of fungal-, bacterial- and total-SIR with fungal and bacterial biomass. Neely *et al.* (1991) found that SIR on five plant residues in a no-till cropping system was inversely related to the initial C-to-N ratio and was a good predictor of litter biomass remaining. Furthermore, residue decomposition rates were positively related to the total SIR averaged across dates. They suggested that decomposition rates for plant litter might be predicted from SIR measurements. The contributions of fungi and bacteria to the decomposition process have been followed using SIR, with the addition of selective inhibitors, in the soil (Anderson and Domsch, 1975), in the rhizosphere (Nakas and Klein, 1980) and on residues (Beare *et al.*, 1990, 1991; Neely *et al.*, 1991). Anderson and Domsch (1975) included the selective inhibitors streptomycin and cycloheximide to determine prokaryotic and eukaryotic contributions, respectively, to total SIR in soils. Beare *et al.* (1990) optimized conditions for the use of streptomycin and cycloheximide for maximum selective inhibition of SIR on plant residues. They showed that inhibition of respiration rates was greatest within the first 3 h following application of glucose to residues. Increases in res-

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piration rates after 3 h were attributed to biomass synthesis. They concluded that the procedure was satisfactory for identifying the relative contribution of fungi and bacteria to SIR on decomposing residues within a short-term assay.

In agricultural environments, microbial communities appear to respond rapidly to conditions favorable for decomposition. Microbial biomass therefore may be a more direct predictor of litter decomposition rates than resource quality because the microbial biomass integrates the effects of both resource quality and climate (Wardle, 1992). Substrate induced-respiration should reflect temperature, water availability and resource quality effects on microbial communities at a given time because optimum conditions result in growth, whereas periods of stress result in reduced growth and death. The relationship developed by Neely *et al.* (1991) between SIR and decay rate (k) potentially represents an important new tool for determining decomposition rates for various residues within moderate environments without the need for laborious and prolonged mass loss measurements. Our principle objective was to evaluate the potential of SIR to serve as a predictor of residue decomposition coefficients using the equation proposed by Neely *et al.* (1991).

MATERIALS AND METHODS

Microbial respiration and decomposition of five crop residues were determined monthly from September 1991 to August 1992. The study was conducted on a Pullman clay loam (fine, mixed, thermic Torrertic Paleustoll) at the USDA-ARS Conservation and Production Research Laboratory, Bushland, Texas. The plant material consisted of leaf and stem residues of alfalfa (*Medicago sativa* L.), corn (*Zea mays* L.), grain sorghum (*Sorghum bicolor* (L.) Moench), winter wheat (*Triticum aestivum* L.), and a solid culm spring wheat. Alfalfa was harvested at full bloom during early July 1991, and could be considered green manure. Corn residue was collected from irrigated corn plots following harvest for grain during the fall of 1990. Grain sorghum residue was collected from irrigated plots during the late grain fill stage in the fall of 1990. The solid culm spring wheat and winter wheat residues were collected during the last week of June 1991, 1 week prior to wheat harvest. All residues were dried for 3–5 days at 55–60°C at the time of collection and again for 1 day at 55°C prior to processing. The residues were chopped into 6- to 9-cm lengths and weighed (20 g) into 10 × 10-cm, 1-mm mesh polypropylene bags. The residues were placed within three water regime plots which were part of a larger experiment described by Steiner *et al.* (1994). The three water regimes were established as follows: (1) 50-mm irrigation applied at 7- to 21-day intervals during the spring and summer; (2) 50-mm irrigation applied every other time that treatment 1 received irrigation; and (3) no irrigation. There were three replications of each water regime. The plots measured 12 × 22 m. Twelve bags of each residue were placed on the soil surface, between rows of standing wheat residue, in each of the three replicate plots on 31 July 1991. Soil temperature was monitored daily, and residue and soil moisture were determined gravimetrically and periodically during the experiment.

Respiration measurements

Measurements of basal respiration, total SIR (TSIR), fungal SIR (FSIR) and bacterial SIR (BSIR) (Beare *et al.*, 1991) were used to evaluate microbial activity on the residues over 1 y. At monthly intervals, residue bags were removed from each replicate and returned to the laboratory, where they were held at 4°C for processing. Residues were removed from the bags, weighed and coarsely chopped in a mini-food processor. Subsamples (1–2 g) were weighed for moisture determination (2.5 h at 100°C and again after 24 h). After the 2.5-h moisture content was determined, 1-g subsamples (dry-weight basis) were weighed into five 250-ml Erlenmeyer flasks for use in the SIR measurements. There were five treatments: (1) basal respiration (2.5 ml H_2O); (2) total SIR (2.5 ml H_2O); (3) fungal inhibition (2.5 ml cycloheximide solution, 16 mg ml^{-1}); (4) bacterial inhibition (2.5 ml streptomycin solution, 3.2 mg ml^{-1}); and (5) double inhibition (2.5 ml cycloheximide + streptomycin). The residues were refrigerated overnight at 4°C after addition of the treatments.

On the following day, samples were removed from the refrigerator every 6 min and equilibrated to room temperature 25°C (36 min). Glucose (2.5 ml, 16 mg ml^{-1}) was then added to each flask, except the basal respiration treatments, which received 2.5 ml distilled H_2O. The flasks were placed inside an incubator (22°C) and attached to a manifold that supplied CO_2-free humidified air at 250 ml min^{-1}. The flow-through system eliminated CO_2 that accumulated before incubation. The rate of CO_2 evolution was determined with an infra-red gas analyzer (LI 6200, LI-COR Inc. Lincoln, NE). The concentration of CO_2 flowing through the analyzer from the sample was integrated for 60 s after reaching apparent steady-state conditions. Measurements were made within 1–2 h following addition of glucose to avoid increases in microbial respiration due to significant population growth and were made within the optimum 3 h period indicated by Beare *et al.* (1990).

Total SIR (TSIR) is the amount of CO_2 evolved from flasks receiving the glucose treatment (Beare

et al., 1990). The contribution of fungi to SIR was estimated as FSIR = TSIR − Cy, where Cy is the respiration from cycloheximide-treated residue, and the contribution of bacteria to SIR was estimated as BSIR = TSIR − St, where St is the respiration on streptomycin-treated residues. The fungal-to-bacterial ratio was calculated as fungal-SIR-to-bacterial-SIR.

Mass loss

The mass loss of the residues was estimated from the fresh weight and moisture content of the residues measured at sampling (24 h, see above). Subsamples of the residues were ground and then ashed in a muffle furnace at 475°C for 4 h to determine ash content. All fresh weights were corrected to ash-free dry weights.

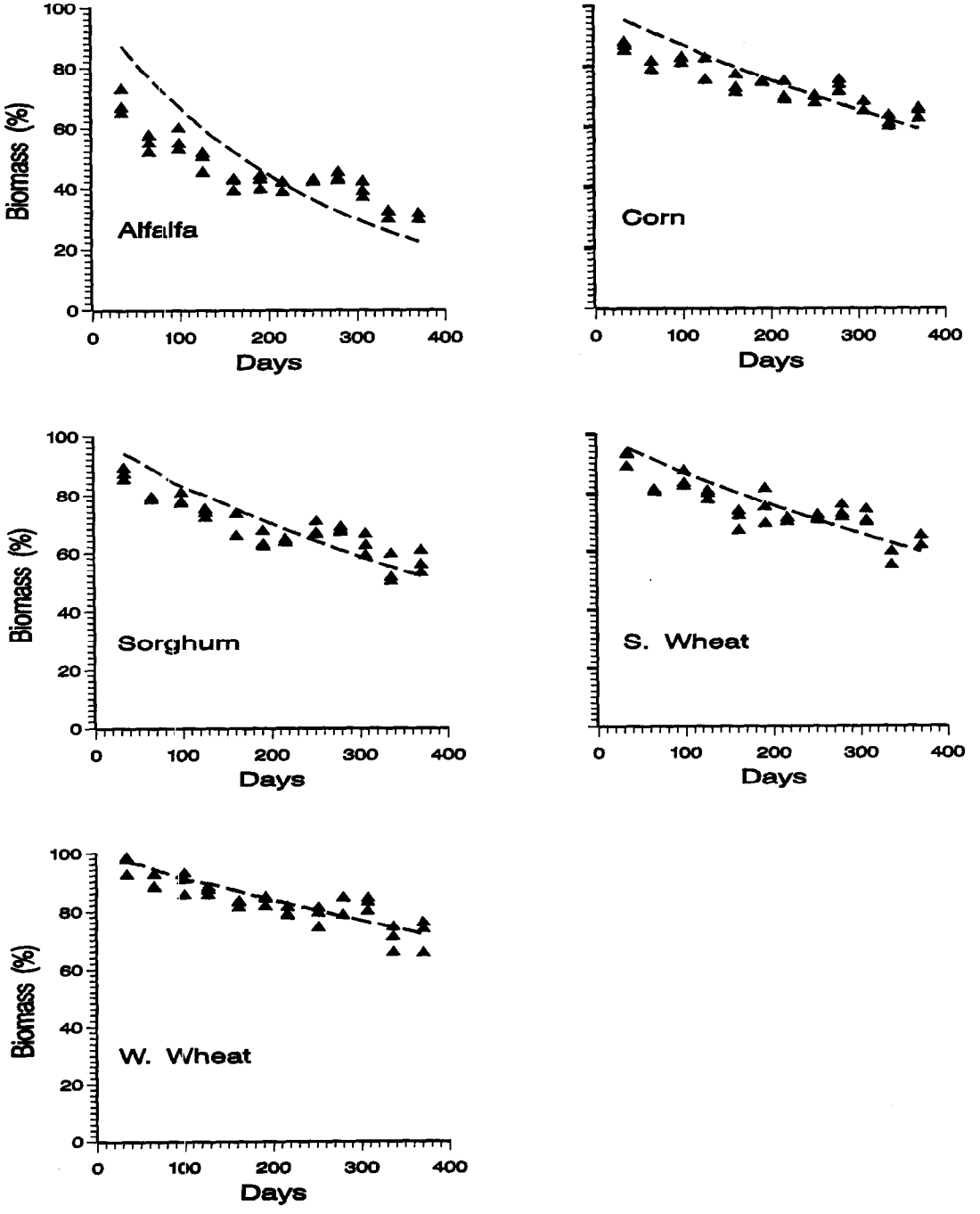

Fig. 1. Mass loss for alfalfa, corn, grain sorghum, spring wheat and winter wheat residues decomposing on the soil surface at Bushland, TX. Triangles represent the means for each irrigation treatment, and the lines were fitted to the data using equation 1.

Statistical analysis

The ash-free dry weights were used for determining crop decomposition rate coefficients (k) by nonlinear regression. A single exponential decay equation was fitted for each crop-replication combination using the MODEL procedure in SAS/ETS (SAS Institute Inc., 1988). The decay equation,

$$M_t = M_0 \exp^{(-k \times \text{time})}, \quad (1)$$

predicts M_t, mass (g) remaining at time t, based on M_0, the initial mass (g), k (d^{-1}) and time (d). The k values were used in an analysis of variance (PROC GLM) to determine differences due to residue type and irrigation (SAS Institute Inc., 1989). Relationships between k and TSIR, and between TSIR and basal respiration were evaluated using regression analysis (Freund *et al.*, 1986).

RESULTS AND DISCUSSION

Irrigation treatments did not affect residue decomposition rates or the microbial respiration measurements. This result is somewhat surprising since previously we had used irrigation as a means to increase the number of water regimes in studies of residue decomposition at this location (Schomberg *et al.*, 1994). Two factors probably combined to produce the observed lack of irrigation effects on decomposition. The first was the tendency for rain to occur soon after an irrigation event, and the second was that the residue bags were placed in plots that contained large amounts of small grains residue that reduced the rate of drying and suppressed temperature fluctuations. Since irrigation effects were not significant, the irrigation treatments were used as additional replicates in the regression analysis.

Mass loss

Mass loss from the crop residues over the 12 months is shown in Fig. 1. Decomposition coefficients (k) for mass loss decreased in the order alfalfa > grain sorghum > corn = spring wheat > winter wheat (Table 1). This trend is similar to the total N and C-to-N relationships observed for the initial crop residues. Similar trends for faster decomposition of forage legume residues than for grain crop residues have been observed by Broder and Wagner (1988), Neely *et al.* (1991) and Schomberg *et al.* (1994). The faster decomposition is generally attributed to the greater N and lower lignin contents of legumes compared to the grain crops.

Table 1. Initial crop residue chemical properties and decomposition coefficients (k)

Crop	Percentage N	Percentage ash	C-to-N[†a]	k
Alfalfa	3.88	9.61	9.5	−0.0041 A[b]
Corn	1.10	7.49	34.5	−0.0014 C
Grain sorghum	1.22	12.77	29.3	−0.0017 B
Spring wheat	0.96	12.82	37.2	−0.0014 C
Winter wheat	0.77	10.11	47.9	−0.0009 D

[a]C-to-N ratio calculated based on C content of the residue = 41%.
[b]Means followed by different letters are significantly different, as indicated by the Waller Duncan means separation test ($\alpha = 0.05$).

SIR changes over time

Patterns of microbial activity as indicated by basal respiration, TSIR, FSIR and BSIR were different among the five crop residues (Fig. 2). Although patterns of respiration activity were different through time and across residues, the trend among the residues was for alfalfa > grain sorghum > corn = spring wheat > winter wheat. During the course of decomposition, TSIR changed the most for alfalfa and grain sorghum residues. The greater changes in TSIR for these residues reflect the higher initial N contents, which probably promoted rapid microbial colonization and decomposition activity. Fungal-SIR declined for all five residues over the last 6 months, whereas BSIR tended to remain constant over the 12 months. This resulted in a decreasing FSIR-to-BSIR ratio over the last 6 months for most of the residues. However, the FSIR-to-BSIR ratio generally remained greater than 1, indicating that fungi contributed more to residue decomposition than bacteria.

On alfalfa residues, basal respiration and TSIR declined through the 12 months, with basal respiration decreasing at a faster rate than TSIR (Fig. 2). Fungal-SIR for alfalfa followed a similar trend to basal respiration and TSIR after the second measurement in October. Bacterial-SIR remained constant through the 12-month period. Decreasing basal respiration, TSIR and FSIR for alfalfa indicate that microbial activity and community size decreased at the same time residue mass and decomposability of the residues decreased.

Corn and grain sorghum residues basal respiration, TSIR, FSIR and BSIR increased during the first 5–6 months and then declined during the rest of the study (Fig. 2). Changes in microbial activity were more apparent on grain sorghum than on corn, but followed a quadratic response for both crops. The period of increasing microbial respiration rates represents increasing colonization by microorganisms, whereas the availability of substrates later in the study probably limited respiration.

Respiration measurements on spring wheat and winter wheat residues remained somewhat constant and were similar throughout the 12 months (Fig. 2). Basal respiration for spring and winter wheat responded similarly to that for corn and grain sor-

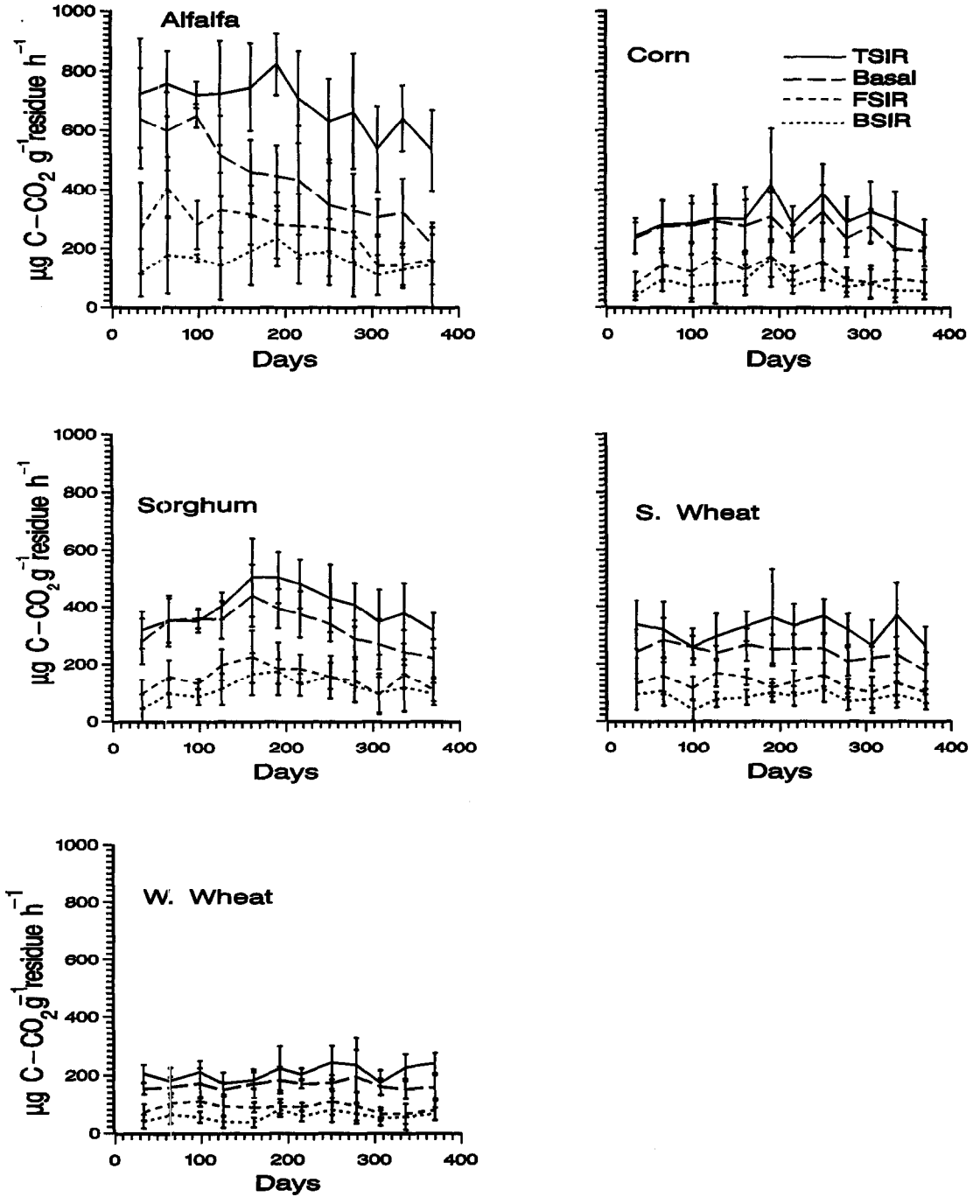

Fig. 2. Total substrate-induced respiration (TSIR), fungal-SIR, bacterial-SIR and basal respiration on the five crop residues. Plotted points are means (n = 9) and bars represent one standard deviation.

ghum. Total SIR increased slightly for winter wheat, while remaining constant for spring wheat. Fungal- and bacterial-SIR varied between the two residues, but overall changed very little during the year. The smaller change in microbial respiration on the wheat residues reflects the lower resource quality of small grains residues (Table 1).

The FSIR and BSIR measurements did not add up to TSIR for any of the residues and indicated that total inhibition of bacteria or fungi was not possible with the antimicrobial agents. Beare *et al.* (1990) showed that total inhibition averaged 88% with little variation between residues. Nakas and Klein (1980) also observed that the additive effect of streptomycin and cycloheximide on rhizosphere and rhizosplane microbial populations equalled 88% but was within 10% of the combined use of both antibiotics. They attributed the remaining glu-

cose mineralization activity to a portion of the microbial population unaffected by the use of either antibiotic. Other limitations to the use of antibiotics for distinguishing microbial groups have been discussed by Parkinson *et al.* (1971). Differences in respiration response between bacteria and fungi may not reflect actual contributions to residue mineralization because of differential glucose utilization. Nakas and Klein (1980) indicate that overall residue mineralization may be more affected by fungi because of their capacity to produce enzymes capable of polymeric cleavage, which would be more important in the degradation of substrates, such as starch, hemicellulose and cellulose.

C status of residues

Basal respiration reflects the overall activity or energy expenditure of the microbial biomass (Anderson and Domsch, 1985) and is also considered to reflect the availability of slow-flowing C for microbial maintenance in soils (Insam *et al.*, 1991). Basal respiration could be used to indicate C availability from crop residues, whereas TSIR indicates the size of the microbial biomass. The basal respiration expressed as a percentage of TSIR should indicate the 'relative C status' of the microbial community and is presented for the five residues in Fig. 3. The ratio decreased with time for all five residues. The greatest decrease occurred for alfalfa residues, whereas the other four residues had similar smaller decreases. On several dates during the early part of the study, basal respiration was equal to or slightly greater than TSIR for corn and grain sorghum.

Several researchers have used specific respiration (qCO_2, as unit CO_2 unit^{-1} $C_{microbial\ biomass}$ h^{-1}) to evaluate soils and management effects on soil microbial biomass (Anderson and Domsch, 1985, 1990, 1993; Insam and Haselwandter, 1989; Insam *et al.*, 1991) and as an indication of the C utilization efficiency of the microbial biomass. Relatively young microbial cells are considered to be metabolically more active and therefore exhibit a higher qCO2 (Insam *et al.*, 1991). In agricultural soils, a high qCO2 indicates that nutrient turnover is accompanied by high rates of C loss (Insam *et al.*, 1991). Insam and Haselwandter (1989) demonstrated that ecosystem succession is accompanied by a decrease in the specific respiration (more developed soils evolved less respiratory CO_2 per unit maintained microbial biomass C than young soils). Our data for relative respiration for the decomposing residues indicate that microbial community changes were more rapid on easily-degradable materials (alfalfa vs. other residues) and that decomposition resulted in changes similar to those found by Insam and Haselwandter (1989). Decreases in relative respiration reflect the increasing complexity of

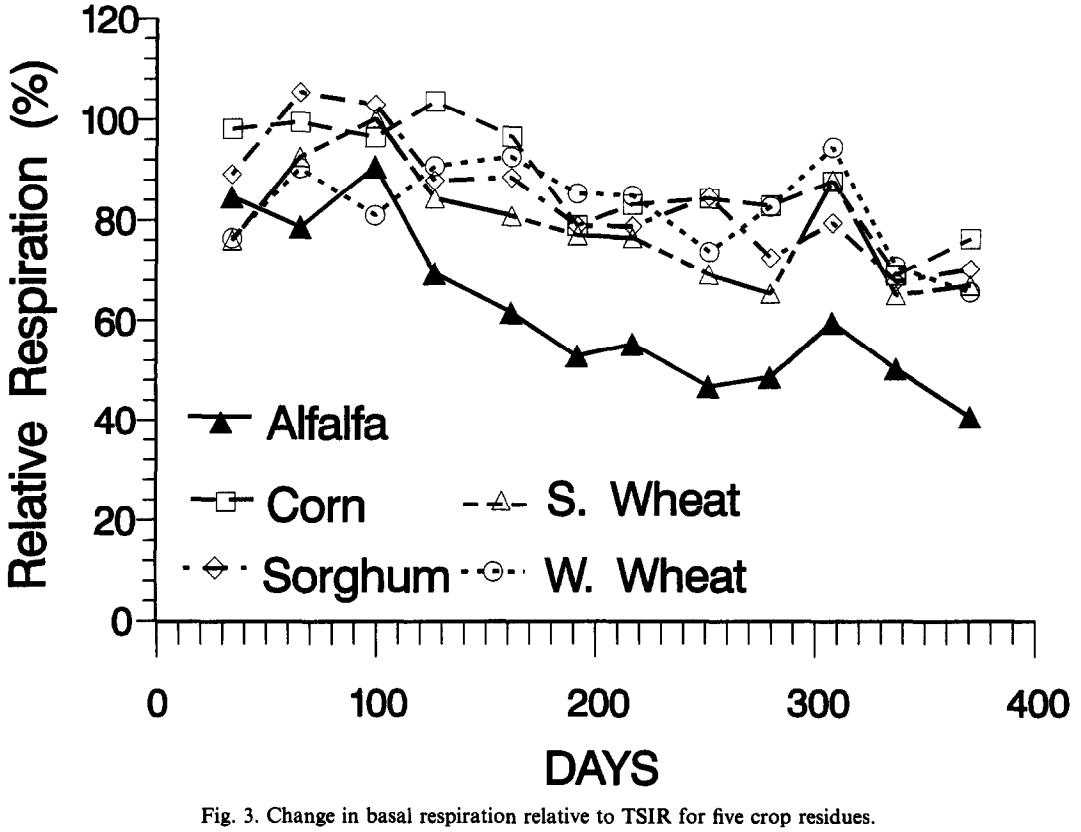

Fig. 3. Change in basal respiration relative to TSIR for five crop residues.

the chemical constituents in the remaining residue, and the declining FSIR-to-BSIR ratio with time indicated a shift in the composition of the microbial community accompanying the changes in residue quality.

Our respiration results are different from those of Neely *et al.* (1991). They observed greater variation between sample dates for TSIR measurements on crimson clover (*Trifolium incarnatum* L.), hairy vetch (*Vicia villosa* Roth), and crabgrass (*Digitaria sanguinalis* (L.) Scop.). They recorded that the total SIR for these crop residues first decreased and then increased during their study. The total SIR response for sorghum residues in their study was close to that observed in our study. In contrast to our observation of similar patterns between TSIR and FSIR, their measurements of FSIR followed TSIR only for three dates, whereas both studies indicated that BSIR showed no consistent pattern across residues or dates. Their FSIR-to-BSIR ratio indicated the dominance of fungi on the decomposing residues. Differences in microbial response between the two studies are probably related to environmental and microbial community differences between the two locations.

Predicting residue decomposition from TSIR

Because microbial activity is responsible for the major portion of mass loss from decomposing residues, in most agricultural systems, measurement of microbial biomass should be directly related to mass loss. Neely *et al.* (1991) showed that residue decomposition could be related to TSIR measurements for five plant residues; crimson clover, hairy vetch, grain sorghum, crabgrass and oak leaves (*Quercus prinus* L.). They proposed an equation relating residue decomposition coefficients to the average TSIR measurement made four times during their 160-day study. We used their equation to predict k from our TSIR data averaged for the 12 months, but the results were not satisfactory (Fig. 4). Regression of the observed vs. predicted

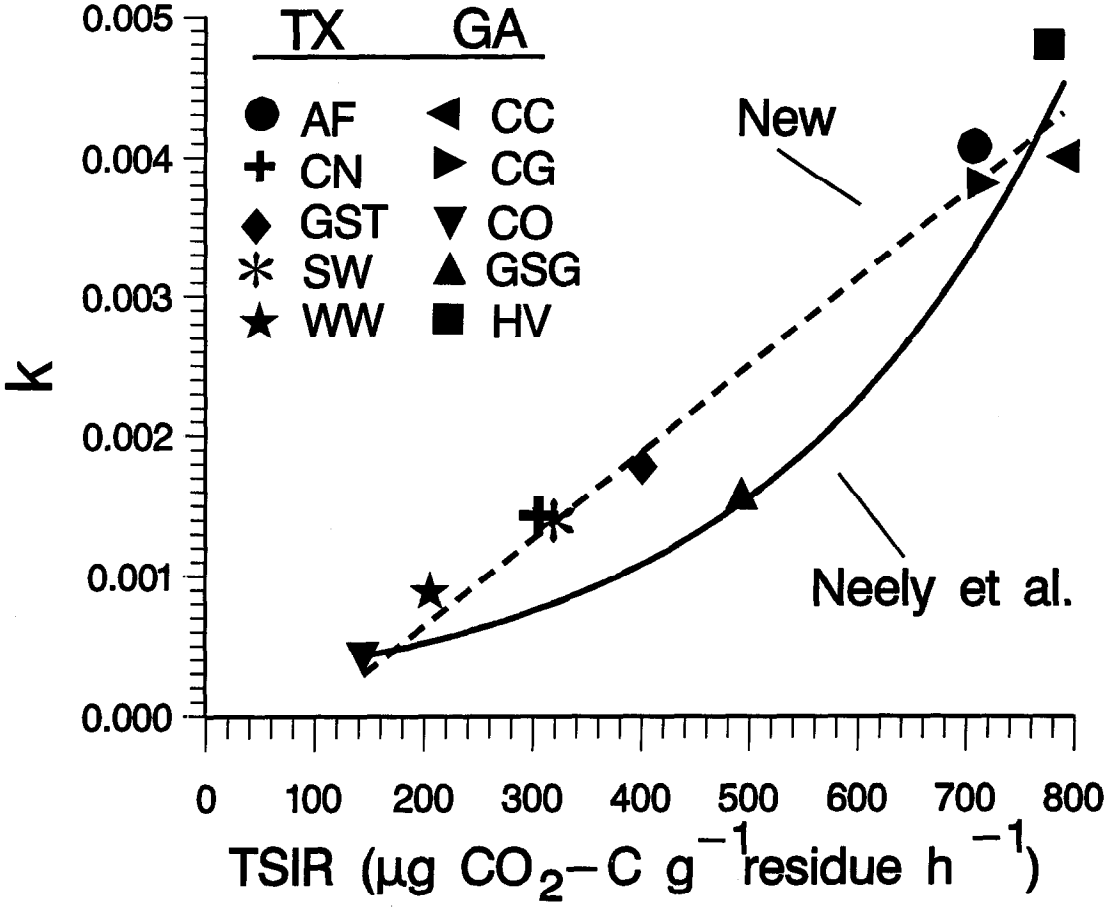

Fig. 4. Prediction of residue decomposition coefficients for crop residues using the equation $-k = 0.095 \times 10^{0.0016 \times \text{TSIR}}$ (Neely *et al.*, 1991) and a new equation, $-k = -6.07 \times 10^{-4} + 6.23 \times 10^{-6} \times \text{TSIR}$ [developed from the data collected in this study and the data from Neely *et al.* (1991)]. Residues from TX were AF = alfalfa, CN = corn, GST = grain sorghum, SW = spring wheat, WW = winter wheat. Georgia residues were CC = crimson clover, CG = crabgrass, GSG = grain sorghum, HV = hairy vetch, CO = chestnut oak (Neely *et al.*, 1991).

values indicated an $R^2 = 0.89$ and a slope equal to 0.88. Neely *et al.* (1991) indicated that their equation may be somewhat limited because it is developed from only five species. We combined our data with that of Neely *et al.* (1991) and found that a linear equation could be used to describe the relationship between k and average TSIR (Fig. 4) for the 10 types of residues. Based on linear regression and a Chi-square evaluation of the combined data, the difference between the two equations was small ($R^2 = 0.94$ for both equations). The fit of the data is somewhat surprising because of the climatological differences between the two studies (humid vs. semi-arid) and differences in residues. Our analysis indicates a positive linear relationship between decomposition and glucose-inducible microbial respiration (TSIR) or the size of the residue-borne microbial community.

The relationship between TSIR and k could be used to determine decomposition coefficients on residues allowed to decompose *in situ* for a short period. The procedure would allow for the determination of crop and environmental specific k values at various locations without intensive mass loss sampling. Although no additional data sets were available to evaluate this hypothesis or the accuracy of the new relationship for predicting decomposition rates, we illustrate the possible usefulness with the TSIR measurements made on day 60 (Fig. 5). Data from each of the irrigation treatments are plotted separately to give an indication of variability. Even though the data are not independent, they indicate a slight underprediction of decomposition rates for most of the residues. Results might be improved by using an equation developed using TSIR measurements from early on during decomposition. Combining our data for TSIR on day 60 with those of Neely *et al.* (1991) on day 52 produced a slightly different equation with a zero intercept and relatively good fit ($-k = \text{TSIR} \times 5.55 \times 10^{-6}$, $R^2 = 0.96$). However, caution should be used before using this equation since we have no additional data for validation.

Further research is needed to verify that TSIR, along with these equations, provides a useful tool for predicting residue decomposition. The technique could help improve the understanding of microbial dynamics on decomposing residues when applied across different environmental conditions or agroecosystems. Total SIR on plant residues appears to reflect accurately the dynamic response of the

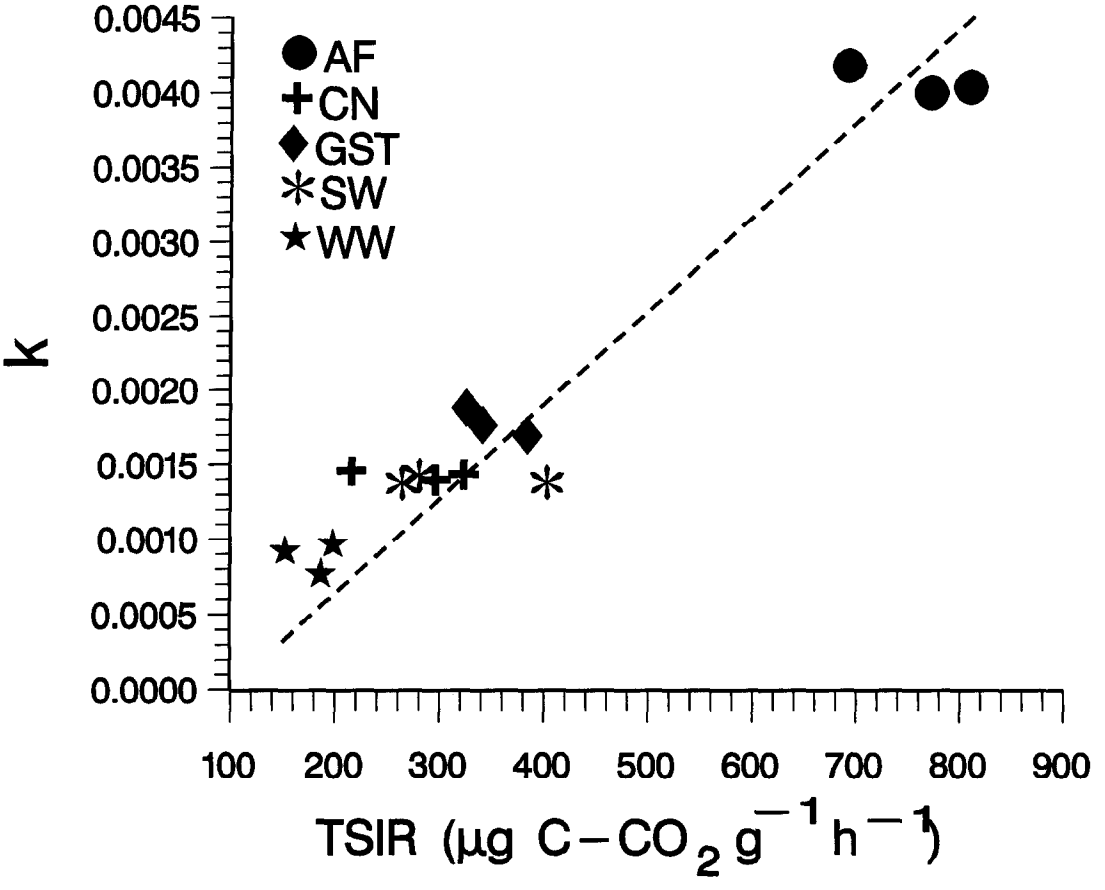

Fig. 5. Prediction of decomposition coefficients using the new equation presented in Fig. 4 from the TSIR measurements made on day 60 in the Bushland, TX study.

microbial community to resource quality and climatic conditions during decomposition.

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