Published online August 3, 2006

Maize Root Biomass and Net Rhizodeposited Carbon: An Analysis of the Literature

B. Amos and D. T. Walters*

ABSTRACT

Assessment of net primary productivity of maize (*Zea mays L.*)-based agroecosystems is dependent on both above and belowground dry matter production that is ultimately returned to the soil as residue and decaying roots. Root to shoot ratio (R/S) is a parameter often used to estimate root biomass (RB) when shoot biomass is measured or estimated. The labor intensive nature of root sampling and wide variety of sampling techniques has lead to a paucity of maize RB data in the literature, and few researchers have endeavored to characterize R/S throughout an entire growing season. In this paper, the results of 45 maize root studies published in 41 journal articles are summarized and the data used to generate estimates of maize RB and R/S versus days after emergence (DAE). The data from these studies indicate that on average, RB was maximized just after anthesis at approximately 31 g plant^{-1} (13.6 g C plant^{-1}) and that average R/S varied from a high of 0.68 at emergence to a low of 0.16 at physiological maturity. Net rhizodeposited C as a percentage of total net root-derived belowground C at time of sampling (%NRC) was reported for 12 maize studies and varied between 5 and 62%. The wide variation in the %NRC was shown to be highly correlated with an index combining irradiance level, photoperiod, and ambient temperature, suggesting a strong dependence of net rhizodeposited C on rate of photosynthesis and soil respiration. The net belowground C deposition at maize physiological maturity is estimated as 29 ± 13% of shoot biomass C for maize that has not experienced stress.

WORLDWIDE PRODUCTION of maize now surpasses that of wheat and rice (U.S. Census Bureau, 2002), making it one of the most important food sources for a growing population. Maize is currently planted on over one fifth of the world's agricultural land devoted to cereal production, an area that covers approximately 137.6 million hectares (Food and Agricultural Organization, 2002). It has been suggested that cropland has a strong potential to mitigate the greenhouse effect by sequestering C in the soil (Lal et al., 1998), and to assess this potential, it is important to quantify the contributions of both the above and belowground structures of various crops as root derived C is likely a primary source for replenishment of soil organic C (SOC) lost to heterotrophic respiration (Balesdent and Balabane, 1996; Bolinder et al., 1999; Gale and Cambardella, 2000). Due to its large and extensive root system, maize, in particular, has the potential to sequester C through belowground inputs. In a 3-yr study, Buyanovsky and Wagner (1986) showed that the post-harvest C input to the soil from maize roots was more than twice that of wheat or soybean roots. There is a need, however, to more accurately characterize seasonal maize root growth, particularly as it relates to plant phenology. Such information would be useful as an input in nutrient uptake, C allocation, and ecosystem modeling, as well as in regional estimates of root C deposition and net primary productivity (Verma et al., 2005) in the extensive land area devoted to maize production worldwide. Unfortunately, destructive root sampling along with the processing of root material collected in field studies is an extremely labor intensive endeavor, making the measurement of root growth throughout the growing season unfeasible for most research efforts. Because of the difficulty in sampling RB and, in the case of field measurements, the added problem of scaling point measurements to a field scale, there is a wide variation in biomass values reported in the literature. Direct measurements of root characteristics are far more easily accomplished in the greenhouse or growth chamber, and while these studies provide necessary data related to root processes, they are rarely extended over the entire life of the maize plant and may not reflect the root system as it would exist under field conditions. In both field and controlled studies, there is also an appreciable amount of rhizodeposited C resulting from the exudation of organic compounds, sloughing of root cells, root cap mucigels, and root turnover that is not easily quantified.

The objectives of this paper are to (i) provide a brief review of root sampling methodologies employed in estimating RB, (ii) collate published literature of the past 30 yr of measured maize RB and R/S ratio and derive a generalized relationship between maize development stage, RB, and R/S ratio (iii) provide a summary of quantitative data published regarding additional net belowground maize C allocation that is not measurable through root sampling, that is, sloughed off root material, and exudation.

MEASUREMENT OF ROOT BIOMASS

Confined Destructive Methods

In this paper, the discussion of root sampling methods will be limited to quantitative destructive methods that produce a physical measurement of RB. These are the methods that have been used in the studies reported in Table 1.

Root biomass sampling methods in which the entire root system is confined (e.g., in pots, nylon mesh, wire netting, etc.), have several obvious advantages: the entire root system may be sampled with relative ease and

B. Amos, and D.T. Walters, University of Nebraska-Lincoln, Department of Agronomy and Horticulture, Lincoln, NE 68583-0915. A contribution of the University of Nebraska Agricultural Research Division, Lincoln, NE 68583. Journal Series No. 14604. *Corresponding author (dwalters1@unl.edu).

Published in Soil Sci. Soc. Am. J. 70:1489–1503 (2006).
Review & Analyses and Soil Biology & Biochemistry
doi:10.2136/sssaj2005.0216

677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: DAE, days after emergence; GDD, growing degree days; HI, harvest index; %NRC, net rhizodeposited carbon expressed as percentage of total net root-derived carbon; PPFD, photosynthetic photon flux density; PAR, photosynthetically active radiation; R/S, root to shoot ratio; RB, root biomass; SOC, soil organic carbon.

Table 1. Maize root (RB) and shoot biomass and root/shoot ratios (R/S) summarized from 45 studies.

Reference	Study type	Plant population	Root sampling method	Time of sampling†	Growth stage†	Treatment	RB	Shoot biomass	R/S
		plants ha^{-1}					g plant^{-1}		
Allmaras et al., 1975	field	70 900	monolith	47 DAP			2.95	16.0	0.18
				59 DAP			12.16	30.1	0.40
				73 DAP			22.11	88.9	0.25
				87 DAP			23.28	132.6	0.18
Anderson, 1988	field	62 000 (seeding rate)	cores	8 WAP	V10-V12	0 kg N ha^{-1}	32.5‡	40.5‡	0.93‡
				8 WAP	V10-V12	180 kg N ha^{-1}	37.5‡	98.5‡	0.41‡
				11 WAP	R1	0 kg N ha^{-1}	43.0‡	115‡	0.40‡
				11 WAP	R1	180 kg N ha^{-1}	38.5‡	204‡	0.20‡
				15 WAP	R4	0 kg N ha^{-1}	43.5‡	162‡	0.30‡
				15 WAP	R4	180 kg N ha^{-1}	43.0‡	319‡	0.14‡
Bonifas et al., 2005	field§	10 000	confined root		VE-V6	0 g N pot^{-1}			0.71
					VE-V6	1 g N pot^{-1}			0.69
					VE-V6	3 g N pot^{-1}			0.66
		50 000			VE-V6	0 g N pot^{-1}			0.85¶
					VE-V6	2 g N pot^{-1}			0.64¶
					VE-V6	6 g N pot^{-1}			0.59¶
		10 000			V6-V13	0 g N pot^{-1}			0.61
					V6-V13	1 g N pot^{-1}			0.54
					V6-V13	3 g N pot^{-1}			0.42
		50 000			V6-V13	0 g N pot^{-1}			0.72¶
					V6-V13	2 g N pot^{-1}			0.67¶
					V6-V13	6 g N pot^{-1}			0.56¶
		10 000			V13-V16	0 g N pot^{-1}			0.36
					V13-V16	1 g N pot^{-1}			0.41
					V13-V16	3 g N pot^{-1}			0.36
		50 000			V13-V16	0 g N pot^{-1}			0.57¶
					V13-V16	2 g N pot^{-1}			0.55¶
					V13-V16	6 g N pot^{-1}			0.51¶
		10 000			V16-R2	0 g N pot^{-1}			0.28
					V16-R2	1 g N pot^{-1}			0.24
					V16-R2	3 g N pot^{-1}			0.30
		50 000			V16-R2	0 g N pot^{-1}			0.70¶
					V16-R2	2 g N pot^{-1}			0.51¶
					V16-R2	6 g N pot^{-1}			0.46¶
Crozier and King, 1993	field	62 000 (seeding rate)	cores		R1				0.27
Durieux et al., 1994	field	43 000	cores		20 DB R1	low precipitation	20.41#		
					20 DB R1	high precipitation	44.60#		
					R1	low precipitation	40.54#		
					R1	high precipitation	61.72#		
					R6	low precipitation	21.49#		
					R6	high precipitation	58.95#		
Eghball and Maranville, 1993	greenhouse		confined root		V2	0 mg N kg^{-1} soil	0.043		0.420
					V2	30 mg N kg^{-1} soil	0.049		0.421
					V2	60 mg N kg^{-1} soil	0.048		0.453
					V2	90 mg N kg^{-1} soil	0.044		0.446
					V9	0 mg N kg^{-1} soil	11.43		0.438
					V9	30 mg N kg^{-1} soil	9.39		0.337
					V9	60 mg N kg^{-1} soil	9.37		0.301
					V9	90 mg N kg^{-1} soil	9.43		0.304
	field	44 500 – 62 000	excavation		V2		0.0725#		0.407#
			cores		VT	0 kg N ha^{-1}	26.3		0.193
					VT	60 kg N ha^{-1}	25.1		0.159
					VT	120 kg N ha^{-1}	19.5		0.128
					VT	180 kg N ha^{-1}	20.7		0.145
Fageria, 2002a	greenhouse		confined root	4 WAP		48 % base sat.	0.88††	2.28††	0.39††
				4 WAP		78 % base sat.	0.74††	2.48††	0.30††
				4 WAP		91 % base sat.	0.65††	1.87††	0.35††
				4 WAP		94 % base sat.	0.80††	1.89††	0.42††
				4 WAP		97 % base sat.	0.77††	1.62††	0.47††
Fageria, 2002b	greenhouse		confined root	4 WAP		0 mg Zn kg^{-1}	2.38††		0.97††
				4 WAP		5 mg Zn kg^{-1}	2.08††		0.82††
				4 WAP		10 mg Zn kg^{-1}	2.11††		0.83††
				4 WAP		20 mg Zn kg^{-1}	2.63††		0.99††
				4 WAP		40 mg Zn kg^{-1}	1.96††		0.74††
				4 WAP		80 mg Zn kg^{-1}	2.35††		0.92††
				4 WAP		120 mg Zn kg^{-1}	2.11††		0.92††
				3 WAP		0 mg B kg^{-1}	0.47††		0.69††
				3 WAP		1 mg B kg^{-1}	0.57††		0.29††
				3 WAP		2 mg B kg^{-1}	0.43††		0.25††
				3 WAP		3 mg B kg^{-1}	0.44††		0.22††
				3 WAP		6 mg B kg^{-1}	0.35††		0.24††
				3 WAP		12 mg B kg^{-1}	0.30††		0.21††

Continued on next page.

Table 1. Continued.

Reference	Study type	Plant population	Root sampling method	Time of sampling†	Growth stage†	Treatment	RB	Shoot biomass	R/S
		plants ha^{-1}					g plant^{-1}		
				3 WAP		0 mg Cu kg^{-1}	1.64††		0.67††
				3 WAP		2 mg Cu kg^{-1}	1.73††		0.77††
				3 WAP		4 mg Cu kg^{-1}	1.75††		0.81††
				3 WAP		8 mg Cu kg^{-1}	1.98††		0.81††
				3 WAP		16 mg Cu kg^{-1}	1.50††		0.68††
				3 WAP		32 mg Cu kg^{-1}	1.28††		0.61††
				3 WAP		64 mg Cu kg^{-1}	1.48††		0.66††
				3 WAP		96 mg Cu kg^{-1}	0.48††		1.22††
Fageria and Baligar, 1997	greenhouse		confined root	19 DAP		0 mg P kg^{-1}	0.25††	0.35††	0.70††
				19 DAP		75 mg P kg^{-1}	0.19††	0.76††	0.25††
				19 DAP		150 mg P kg^{-1}	0.16††	0.92††	0.17††
Feil et al., 1990	chamber		confined root		V3	0 mmol N kg^{-1}	0.10‡‡	0.14‡‡	0.70‡‡
					V3	3.75 mmol N kg^{-1}	0.09‡‡	0.15‡‡	0.61‡‡
					V3	13.75 mmol N kg^{-1}	0.08‡‡	0.14‡‡	0.56‡‡
Foth, 1962	field		monolith	23 DAP			0.54	1.1	0.50††
				37 DAP	V7		4.36	11.6	0.38††
				41 DAP			8.32	26.4	0.31††
				47 DAP			12.26	44.7	0.28††
				54 DAP			17.16	87.9	0.20††
				67 DAP			17.68	165.3	0.11††
				80 DAP			24.74	189.3	0.13††
				100 DAP			25.56	274.4	0.09††
Gupta and Kovács, 1974	chamber		confined root		V5				0.66††
Handa et al., 1985	chamber		confined root	8 DAP			0.052††#	0.049††#	1.06††
				13 DAP			0.094††#	0.122††#	0.77††
				18 DAP			0.106††#	0.199††#	0.53††
				23 DAP			0.114††#	0.281††#	0.41††
				28 DAP			0.114††#	0.277††#	0.41††
Hébert et al., 2001	field§		confined root		V10	Sunlight	1.5	3.2	0.45
					V10	Shade	1.4	3.1	0.45
					V12	Sunlight	4.5	9.3	0.49
					V12	Shade	2.5	6.9	0.37
					V15	Sunlight	16.6	30.8	0.53
					V15	Shade	6.4	6.9	0.24
					R1	Sunlight	46.5	102.2	0.46
					R1	Shade	17.5	75.6	0.24
Hocking and Meyer, 1991	greenhouse		confined root	55 DAP	VT	0.5 mol N m^{-3}	4‡‡	10‡‡	0.40‡‡
				55 DAP		2.5 mol N m^{-3}	8‡‡	20‡‡	0.40‡‡
				55 DAP		6 mol N m^{-3}	10‡‡	31‡‡	0.32‡‡
				55 DAP		12 mol N m^{-3}	11‡‡	34‡‡	0.32‡‡
				55 DAP		25 mol N m^{-3}	12‡‡	43‡‡	0.28‡‡
Huber et al., 1989	greenhouse		confined root	4 WAE	V7	0 m*M* KNO_3			0.59††
				4 WAE	V7	20m*M* KNO_3			0.23††
Hunt et al., 1991	chamber		confined root	56 DAE					0.41††
Imai and Murata, 1976			unknown		V9				0.56††
Karunatilake et al., 2000	field	68 000 (seeding rate)	excavation	22-24 DAP		Plow till			0.47††
				22-24 DAP		No till			0.44††
				34 DAP		Plow till			0.09††
				34 DAP		No till			0.09††
				40-42 DAP		Plow till			0.01††
				40-41 DAP		No till			0.01††
				49-51 DAP		Plow till			0.07††
				49-51 DAP		No till			0.08††
				64-67 DAP		Plow till			0.07††
				64-67 DAP		No till			0.06††
King and Greer, 1986	chamber		confined root	111 DAE	R6	high moisture	47	207	0.22††
				111 DAE	R6	medium moisture	46	192	0.24††
				111 DAE	R6	low moisture	35	180	0.19††
Kondo et al. 2000	field		cores	52 DAP					.0111
				73 DAP		low water stress			.069
				73 DAP		high water stress			.047
Lafitte and Edmeades, 1994	field§	53 000	confined root		R1-R2	low fertilizer rate	19.3††#	51††#	0.38††#
						high fertilizer rate	37.7††#	105.3††#	0.36††#
Ma et al., 2003	field	(see treatments)	excavation		V6	69 000 plants ha^{-1}	0.99††	4.9††	0.200
					V6	89, 000 plants ha^{-1}	0.92††	4.7††	0.202
					V8††	69 000 plants ha^{-1}	3.0††	18.8††	0.155
					V8††	89 000 plants ha^{-1}	2.1††	16.0††	0.126
					R1	69 000 plants ha^{-1}	24.5††	108.3††	0.227
					R1	89 000 plants ha^{-1}	17.1††	92.9††	0.181
Maizlish et al., 1980	chamber		confined root	3 DAE		0 ppm N	0.03	0.06	0.50††
				3 DAE		21 ppm N	0.03	0.08	0.38††
				3 DAE		42 ppm N	0.03	0.08	0.38††
				3 DAE		105 ppm N	0.04	0.10	0.40††

Continued on next page.

Table 1. Continued.

Reference	Study type	Plant population	Root sampling method	Time of sampling†	Growth stage†	Treatment	RB	Shoot biomass	R/S
		plants ha^{-1}					g plant^{-1}		
				3 DAE		210 ppm N	0.05	0.11	0.45††
				10 DAE		0 ppm N	0.25	0.17	1.47††
				10 DAE		21 ppm N	0.35	0.29	1.21††
				10 DAE		42 ppm N	0.45	0.42	1.07††
				10 DAE		105 ppm N	0.51	0.59	0.86††
				10 DAE		210 ppm N	0.67	0.84	0.80††
				17 DAE		0 ppm N	0.38	0.24	1.58††
				17 DAE		21 ppm N	0.84	0.75	1.12††
				17 DAE		42 ppm N	1.30	1.34	0.97††
				17 DAE		105 ppm N	1.93	2.40	0.80††
				17 DAE		210 ppm N	2.89	4.49	0.64††
	field		excavation	1 DAE			0.026††	0.034††	0.76††
				4 DAE			0.035††	0.100††	0.35††
				12 DAE			0.327††	0.466††	0.70††
				22 DAE			0.856††	2.256††	0.38††
				29 DAE			1.66††	3.896††	0.43††
Mengel and Barber, 1974	field	59 300	excavation	15 DAP			0.09§§	0.4	0.22††
			excavation	17 DAP			0.14§§	1.7	0.10††
			excavation	19 DAP			0.22§§	1.0	0.22††
			excavation	21 DAP			0.24§§	1.4	0.17††
			cores	23 DAP			0.48§§	3.7	0.13††
			cores	49 DAP			10.2§§	67.5	0.15††
			cores	69 DAP	R1		13.0§§	129.4	0.10††
			cores	82 DAP			16.0§§	194.4	0.08††
			cores	96 DAP			21.0§§	298.6	0.07††
	field	53 600	excavation	21 DAP			0.18§§	0.6	0.30††
			excavation	23 DAP			0.38§§	1.1	0.36††
			excavation	25 DAP			0.56§§	1.3	0.43††
			cores	34 DAP			5.4§§	8.4	0.64††
			cores	42 DAP			12.5§§	30.9	0.40††
			cores	49 DAP			18.6§§	69.4	0.27††
			cores	56 DAP			21.0§§	107.5	0.20††
			cores	71 DAP			37.3§§	199.3	0.19††
			cores	79 DAP	R1-R2		43.7§§	233.8	0.19††
			cores	86 DAP			43.7§§	243.6	0.18††
			cores	93 DAP			33.7§§	296.9	0.11††
			cores	100 DAP			16.5§§	367.9	0.04††
			cores	113 DAP			19.5§§	414.3	0.05††
			cores	132 DAP			16.9§§	435.1	0.04††
Merckx et al., 1986	chamber		confined root	28 DAG			1.63	2.42	0.67††
				42 DAG			18.39	25.53	0.72††
Merckx et al., 1987	chamber		confined root	28 DAG		low fertilizer rate	2.2	3.4	0.65††
				28 DAG		high fertilizer rate	1.5	2.6	0.58††
				35 DAG		low fertilizer rate	8.5	9.8	0.87††
				35 DAG		high fertilizer rate	4.0	7.7	0.52††
				42 DAG		low fertilizer rate	12.7	13.6	0.93††
				42 DAG		high fertilizer rate	14.3	17.4	0.82††
Mollier and Pellerin, 1999	greenhouse		confined root	27 DAG		Control	2.60††	9.42††	0.28
				27 DAG		P-deprived	0.784††	1.29††	0.62
Osaki et al., 1995	field		excavation.	50 DAP		quick-acting fert.			0.36‡‡#
				50 DAP		slow release fert.			0.34‡‡#
				80 DAP		quick acting fert.			0.18‡‡#
				80 DAP		slow release fert.			0.14‡‡#
				108 DAP		quick acting fert.			0.15‡‡#
				108 DAP		slow release fert.			0.10‡‡#
Patterson and Flint, 1980	chamber		confined root	45 DAP					0.25
Piper and Weiss, 1993	field	62 000 (seeding rate)	excavation		V5		0.5		0.17††
					V10		2.7		0.11††
					V17		14.6		0.13††
					R1		24.7		0.13††
					R2		25.8		0.09††
					R5		24.5		0.07††
Richner et al., 1996	field§		confined root		V2	14.6°C			0.78#‡‡
					V2	16.9°C			0.62#‡‡
					V2	18.0°C			0.74#‡‡
					V3	14.6°C			0.64#‡‡
					V3	16.9°C			0.61#‡‡
					V3	18.0°C			0.77#‡‡
					V4	14.6°C			0.69#‡‡
					V4	16.9°C			0.46#‡‡
					V4	18.0°C			0.58#‡‡
Rogers et al., 1983	field		not specified	11WAP			8.7	40.1	0.22
Sionit et al., 1982	chamber		confined root	15 DAP		PPFD 600 μEm^{-2} s^{-1}			0.52‡‡
				30 DAP		PPFD 600 μEm^{-2}s^{-1}			0.23‡‡

Continued on next page.

Table 1. Continued.

Reference	Study type	Plant population	Root sampling method	Time of sampling†	Growth stage†	Treatment	RB	Shoot biomass	R/S
		plants ha^{-1}					—— g plant^{-1} ——		
				38 DAP		PPFD 600 μEm^{-2}s^{-1}			0.14‡‡
				43 DAP		PPFD 600 μEm^{-2}s^{-1}			0.11‡‡
				25 DAP		PPFD 1200 μEm^{-2}s^{-1}			0.38‡‡
				31 DAP		PPFD 1200 μEm^{-2}s^{-1}			0.25‡‡
				54 DAP		PPFD 1200 μEm^{-2}s^{-1}			0.20‡‡
Stryker et al., 1974	chamber		confined root	42 DAE		12.5 ppm P	11.8‡‡#	48‡‡#	0.25‡‡#
				42 DAE		50 ppm P	12.2‡‡#	52.3‡‡#	0.23‡‡#
Taylor et al., 1996	chamber		confined root	45 DAP		nonparasitized			0.32‡‡
				45 DAP		parasitized			0.99‡‡
Thom and Watkin, 1978	field§	96 900	confined root	69 DAP		0 kg N ha^{-1}	13.6		
				69 DAP		168 kg N ha^{-1}	8.3		
				69 DAP		672 kg N ha^{-1}	12.2		
				127 DAP		0 kg N ha^{-1}	25.3		
				127 DAP		168 kg N ha^{-1}	29.3		
				127 DAP		672 kg N ha^{-1}	29.1		
				180 DAP	R6	0 kg N ha^{-1}	25.9	248.8	0.21††
				180 DAP	R6	168 kg N ha^{-1}	20.9		0.16††
				180 DAP	R6	672 kg N ha^{-1}	20.5		0.14††
Todorovic et al., 2001	chamber		confined root	24 DAP			1.6	2.8	0.57††
				35 DAP			3.5	13.6	0.26††
Tollenaar and Migus, 1984	chamber	80 000	confined root	48 DAP			19.1††	61.1††	0.31††
				63 DAP			27††	105.8††	0.26††
				78 DAP			35.9††	130.4††	0.28††
				91 DAP			31.5††	118.3††	0.27††
				120 DAP			30.4††	115.9††	0.26††
	field§	80 000	confined root	77 DAP		late variety	23.6††	55.5††	0.42††
				96 DAP		late variety	37.1††	151.5††	0.25††
				113 DAP		late variety	38.2††	173.0††	0.22††
				132 DAP		late variety	39.6††	164.3††	0.24††
				162 DAP		late variety	32.0††	119.8††	0.27††
				59 DAP		early hybrid	14.1††	42.0††	0.34
				73 DAP		early hybrid	25.5††	99.9††	0.26
				87 DAP		early hybrid	26.6††	105.1††	0.25
				102 DAP		early hybrid	24.9††	108.9††	0.23
				127 DAP		early hybrid	23.6††	91.1††	0.26
				158 DAP		early hybrid	24.0††	76.8††	0.31
				59 DAP		late hybrid	14.1††	35.0††	0.40
				73 DAP		late hybrid	29.5††	110.8††	0.27
				87 DAP		late hybrid	34.5††	154.1††	0.22
				102 DAP		late hybrid	40.1††	189††	0.21
				127 DAP		late hybrid	40.5††	178††	0.23
				158 DAP		late hybrid	39.1††	151††	0.26
Tubeileh et al., 2003	chamber		confined root	21 DAP		1.30 g cm^{-3} ρ_b	0.37	1.31	0.28
				21 DAP		1.45 g cm^{-3} ρ_b	0.29	1.05	0.28
				35 DAP		1.30 g cm^{-3} ρ_b	2.15	13.0	0.17
				35 DAP		1.45 g cm^{-3} ρ_b	1.27	10.3	0.12
				42 DAP		1.30 g cm^{-3} ρ_b	5.35	27.6	0.19
				42 DAP		1.45 g cm^{-3} ρ_b	3.90	23.5	0.17
Warncke and Barber, 1974	chamber		confined root	18 DAG			0.16	0.36	0.44
				25 DAG			0.29	1.31	0.22
				32 DAG			0.72	4.1	0.18
				39 DAG			2.3	9.6	0.24
				46 DAG			4.6	22.8	0.20
				53 DAG			8.0	39.8	0.20
				60 DAG			8.8	53.5	0.16
				67 DAG			16.0	87.2	0.18
				74 DAG			16.8	95.6	0.18
				81 DAG			17.1	114.0	0.15

† DAP, days after planting; WAP, weeks after planting; DAE, days after emergence; DAG, days after germination; DB, days before; V1, first leaf stage etc.; VT, tasseling; R1, silking; R2, blister; R3, milk; R4, dough; R5, dent; R6, physiological maturity.
‡ Averaged across multiple years.
§ Maize plants grown in containers in field study.
¶ Data from a different growing season.
# Averaged across treatments.
†† Calculated from published data.
‡‡ Estimated from figures.
§§ Estimated from fresh weight assuming a dry weight of 15%.

the sample collected is certain to belong to a particular plant or set of plants. In addition, conditions affecting root growth such as light, temperature, and nutrient status may be easily varied, particularly if plants are cultivated in pots in a greenhouse or growth chamber. This is particularly true for plants grown in solution culture, in which nutrient stress may be applied simply by rinsing the root system and changing the solution (Mollier and Pellerin, 1999) and temperature of both the root and shoot zones are easily controlled (Engels, 1993). A major disadvantage of a confined root system is that the root system produced may be quite different from that

produced under field conditions. For example, maize plants grown in solution culture tend to produce greater root mass and or root length than field-grown maize plants having an equivalent or even larger shoot mass (Maizlish et al., 1980; Warncke and Barber, 1974). However, in a field study, Richner et al. (1996) found no differences among maize plants grown in soil in containers of nylon mesh, PVC, and plants for which root growth was not restricted. Although normally associated with controlled studies, confined root systems may be used in the field for convenience of sampling or to control some environmental condition. Thom and Watkin (1978) inserted wire netting root containers in field plots and grew a single maize plant in each for later root harvest. Hébert et al. (2001) grew maize plants outdoors in 12-L containers to eliminate competition for light, water, and nutrients.

Unconfined Destructive Methods

The most common method of studying maize roots in the field is accomplished through destructive sampling in which all or part of the root system is removed along with the associated soil volume and transported to the laboratory. The advantages of this method are as follows: roots systems are not confined and are growing under normal field conditions, roots may be sampled at any time without removing whole plants, no special equipment needs to be installed at the beginning of the season, sampling depth and spatial pattern is at the discretion of the researcher and may be adjusted as the plant develops, and samples may be collected and frozen for later processing. In destructive sampling representative soil cores are normally taken, although some researchers prefer to excavate the entire root system or some estimated percentage of it (e.g., Piper and Weiss, 1993; Ma et al., 2003). The diameters of cores typically used in maize studies vary, ranging from 0.021 m (Kovar et al., 1992) up to 0.1 m (Kaspar et al., 1991), and this variation is more likely to affect measurements of bulk density than RB. However, the literature suggests that there is a wide variation in depth of sampling, numbers of cores extracted, and pattern of core extraction, which may lead to varability in reported RB. Soil cores are commonly collected from the top 0.3 m of soil in studies of tillage effects on root densities (Crozier and King, 1993; Kaspar et al., 1991; Kovar et al., 1992). However, if the intention of a study is to arrive at accurate estimates of the maize root system over an entire growing season, sampling to greater depths may be more appropriate. The number and spatial pattern of soil cores extracted varies widely among maize studies. Oikeh et al. (1999) assumed a uniform distribution and took cores only at a distance of 0.12 m from the plant. Ewel et al. (1982) extracted soil cores by using randomly selected coordinates. Anderson (1988) took cores directly over a plant, at mid-row, and halfway between the row and the mid-row point. The three previous examples represent sampling schemes that may be adequate when treatment differences in root growth are the primary objective. However, when the objective is to arrive at an accurate estimate of maize RB, a sampling scheme that takes into account the lateral distribution of roots is preferable.

Regardless of the method used to collect destructive root samples, there can be a great time investment in washing the roots and separating live from dead material (Oliveira et al., 2000). For a monolith 0.76-m long, 0.051-m wide, and 3-m deep, Buman et al. (1994) estimated that it took an operator close to 11 h to separate roots from the soil. A small loss of root material may occur during the washing process. This may be due to the loss of root hairs when plants are washed at a young age or to a small loss of decaying root segments when older plants are washed (Böhm, 1979). Oliveira et al. (2000) reported that losses are typically 20 to 40% of the original root weight. However, Böhm (1979) found that this loss of roots from barley plants was never >10% of total root weight when a sieve with a mesh size of 0.5 mm was used. Livesley et al. (1999) recovered almost 95% of the total RB of maize by using a 0.5-mm sieve along with 2.0- and 1.0-mm sieves, while the 2.0- and 1.0-mm sieves alone captured 78% of the total RB at 0- to 15-cm soil depth and 63% at 30- to 45-cm depth.

Measurement of Rhizodeposition

Various labeling techniques have been employed to quantify living root-derived C other than standing RB. This rhizodeposited C can be found in the soil in the vicinity of the living roots, either incorporated into microbial biomass or as nonmicrobial root-derived SOC. Continuous ^{14}C labeling is normally performed in a growth chamber, in which $^{14}CO_2$ of a constant specific activity is supplied to the atmosphere around the shoots (Martens, 1990; Helal and Sauerbeck, 1986). At any stage of development, plant material and soil may be collected and analyzed for total C content using a standard CNS analyzer and ^{14}C content using a scintillation counter. Since labeled SOC can only be root-derived, rhizodeposited C may be quantified in this way. Pulse labeling allows for the study of the belowground translocation of recently fixed C at specific times in plant development. In this method, plants are exposed to an atmosphere containing $^{14}CO_2$ for relatively short periods of time (minutes to several hours) depending on plant age and assimilation rate, during which CO_2 concentration is allowed to decrease (Tubeileh et al., 2003). Plants are then grown under the original conditions, and plant material and soil may be analyzed for total C and ^{14}C content at harvest. This technique may be also used in field studies (e.g., Kisselle et al., 2001).

Another technique that is well suited to both controlled (Qian et al., 1997) and field studies (Balesdent and Balabane, 1992) employs natural ^{13}C abundance. All plants discriminate against $^{13}CO_2$ during photosynthesis, and plants utilizing the C_3 pathway discriminate against the stable ^{13}C isotope more than C_4 plants (Farquhar et al., 1989). The range of $\delta^{13}C$ values for C_3 plants is approximately -32 to -22‰ while that of C_4 plants is -17 to -9‰ (Boutton, 1996). The difference in $\delta^{13}C$ values between C_3 and C_4 plants can be used to determine the amount of SOC originating from maize roots by growing maize plants in soil that has been cropped to predominantly C_3 plants for many years and

has developed a more negative C_3 $\delta^{13}C$ signature. By comparing the $\delta^{13}C$ signature of the uncropped soil to soil cropped to maize, and then combining this information with analysis of total C, the amount of SOC derived from roots of the standing maize crop may be quantified. The natural ^{13}C technique is not as sensitive as artificial labeling with ^{13}C or ^{14}C, and it is important to know the limit of resolution (i.e., the smallest difference between two samples that would be significantly different) before planning an experiment (Balesdent and Mariotti, 1996). Using the natural ^{13}C technique, it was possible to measure the quantity of maize-derived material in a <50-μm soil fraction after one maize crop on a soil developed under C_3 plants (Balesdent and Balabane, 1992; Balesdent and Mariotti, 1996).

Maize Root Distribution

Both depth of sampling and the spatial pattern of samples may affect RB measurements. Dwyer et al. (1996) found that while maize rooting depth at anthesis varied from around 0.7 m to close to 1 m, approximately 90% of the root system was recovered from the top 0.3 m of soil. For soil cores taken to a depth of 0.75 m, Aina and Fapohunda (1986) found that as much as 70% of the total biomass of recovered maize roots was found in the top 0.225 m of the profile at different times of plant growth. Similarly, Osaki et al. (1995) found that 72 to 82% of total root dry weight for maize plants was recovered from the 0- to 0.2-m soil layer. Maize roots are even more concentrated near the soil surface. Crozier and King (1993) found that for 0.3-m deep cores collected in and averaged over tilled and no-tilled plots, 85% of the total root dry matter was present in the 0.01- to 0.15-m layer. Anderson (1988) restricted routine root sampling to a depth of 0.6 m to estimate the size of the maize root system, since they determined that roots in the top 0.6 m accounted for 87% of the total root mass in samples taken up to 1.2 m after grain harvest. Using even deeper (0.8 m) cores, Kondo et al. (2000) detected an increase in the fraction of maize roots below the 0.6-m depth after severe water stress, indicating that stress induced plasticity may necessitate deeper sampling to fully account for belowground biomass.

A sampling pattern based on knowledge of lateral maize root distribution would provide more accurate estimates of maize RB on a per plant basis as well as provide measurements that may be more reliably scaled up to a per hectare basis. Gajri et al. (1994) determined that root length density (cm root cm^{-3} soil) for maize at silking was highest closest to the base of the plant and decreased with distance from the row, then increased somewhat midway between the rows where the root systems of adjacent plants overlapped. Balesdent and Balabane (1992) reported that almost one-half of the RB was located in the 0.2-m wide and 0.2-m deep soil section directly beneath the crown. Clearly, core transect methods must include the zone immediately beneath the plant to obtain quantitative estimates of RB.

It should be noted that in this study, we define RB as that portion of the root system found below the soil surface (i.e., it does not include the aboveground crown). Inclusion of the crown as RB greatly alters this measurement. Balesdent and Balabane (1992) give one of the few reports of the magnitude of aboveground maize root crown biomass (fraction of the maize plant 0.1 m above the soil surface) in relation to belowground RB. In their study, when sampled at physiological maturity, the maize crown contained 29 g C m^{-2} compared with 63.6 g C m^{-2} in standing RB in the upper 0.8 m of soil.

MODELING ESTIMATIONS

Various mathematical models have been constructed that have been used to describe the maize root system. Gerwitz and Page (1974) determined the relationship between total RB and soil depth by taking the reciprocal of the slope of a logarithmic plot of percentage of total roots within a soil horizon plotted against horizon depth. Applying this model to data from two published maize studies, they determined that 63% of the total maize root mass was generally found in the top 0.44 m of soil. A more complex model derived by Hayhoe (1981) provides estimates of plant root weight per depth increment for a given time in days after planting by incorporating a root diffusivity function into a generalized root growth model. Here root diffusivity is a parameter related to characteristics of a soil zone, which include root mass density entering the zone and edaphic factors such as moisture and temperature governing root growth. A nonlinear version of the diffusion equation, dependent on the root weight function as well as on time and vertical distance from the soil surface, provided estimates of maize root weight per depth increment that were much closer to observed values than when root diffusivity was assumed to be a constant. While the models discussed above assume an exponential decrease in root density with depth, CropSyst, a cropping systems simulation model, has a relatively simple approach in which root depth is synchronized with leaf area growth and is assumed to increase linearly to a maximum at the soil surface (Stöckle et al., 2003). Using an input of daily dry matter allocation to the root system provided by another model, Jones et al. (1991) simulated the depth of the maize rooting front and root proliferation in the various soil layers by considering the following limitations to root growth: Al toxicity, Ca deficiency, coarse fragments, which limit water holding capacity, soil strength, poor aeration, and low temperature. Pagès et al. (1989) developed a simulation model that provides projections of the three-dimensional architecture of the maize root system but does not include a C partitioning component. CERES-Maize (Jones and Kiniry, 1986), a widely used simulation model of maize growth, development, and yield, contains a root growth subroutine that calculates the daily growth of the root system in grams $plant^{-1}$. At its simplest level, daily root growth is calculated as the difference between total daily biomass production and the daily growth in weight of other C sinks actively growing during a particular phenological period until grain filling commences. At this point, C not used for grain growth is partitioned equally between the stem and root

system. Hybrid-Maize (Yang et al., 2004), a new model based on the temperature driven growth and development functions of CERES-Maize also incorporates a mechanistic formulation of photosynthesis and respiration to drive assimilate availability. In Hybrid-Maize, the minimum fraction of dry matter partitioned to roots is calculated by a continuous function of growing degree day accumulation from emergence (GDD) until GDD reaches 115% of GDD at silking, at which time allocation of dry matter to roots ceases. Any additional assimilate left after meeting the growth requirements of leaf and stem is partitioned to roots. Spek and Van Oijen (1988) presented a simulation model for root and shoot growth in the vegetative phase that incorporated a light response curve of CO_2 assimilation with a series of Michaelis–Menten equations governing nitrate uptake and the synthesis of amino acids, structural N and structural C. Estimates of R/S ratio from this model for 2-wk-old maize plants subjected to three different NO_3^- treatments for 10 d were approximately 0.18, 0.29, and 0.64 for the high, medium and no NO_3^- treatments, respectively. In another simulation of C assimilation and partitioning in maize, Grant (1989) specified the fraction of assimilated C translocated to the shoot at 0.67 and that to the root at 0.33 before tassel initiation. After tassel initiation, these fractions were then determined on the basis of a phyllochron function by which C allocation is adjusted to account for maintenance and growth respiration before root and shoot dry matter are estimated.

ESTIMATES OF ROOT BIOMASS AND ROOT/SHOOT RATIO

Table 1 contains values of R/S and/or RB at specific sampling times collected from 45 maize studies published in 41 journal articles. Root/shoot ratio is here considered to be the ratio of dry, belowground structural RB to dry, aboveground stover (i.e., stems, leaves, and husks). Assimilate that is lost through exudation, root respiration, or root turnover is not considered as part of RB or R/S in these data. Where R/S values with and without cob plus grain biomass were reported, values without these components were chosen for inclusion in this table. Selection of data from studies involving enhanced atmospheric CO_2 enrichment was limited to the controls, and all studies listed may be assumed to have been conducted under ambient levels of CO_2 concentration. Biomass or R/S values that were calculated from published values are indicated and the method of calculation is presented in this section. As our objective was to examine the change in RB and R/S as a function of time, published reports that did not include the time or phenological stage at sampling are not included in Table 1.

The vast majority of these studies reported biomass on a per plant basis, most commonly grams plant^{-1}, and many of the studies did not provide information allowing for conversion to a per area basis. Therefore, grams plant^{-1} was chosen as the unit of dry matter reported in Table 1. Simple conversions of biomass data as indicated in Table 1 involved dividing by the number of plants when biomass was reported in grams per several plants (Fageria, 2002a, 2002b; Fageria and Baligar, 1997; Lafitte and Edmeades, 1994) and conversion of milligrams to grams (Feil et al., 1990; Handa et al., 1985; Maizlish et al., 1980; Mollier and Pellerin, 1999). Two of the studies listed in Table 1 reported biomass on a per area basis along with plant population, and this information was used to convert biomass to a grams plant^{-1} basis (Ma et al., 2003; Tollenaar and Migus, 1984). For those studies in which a final plant population is given, biomass on an area basis may be obtained by multiplying plant population in plants per hectare by biomass in grams plant^{-1}.

As indicated in Table 1, many of the R/S values were also calculated from published data. Some of the R/S values are simply the reciprocal of a reported shoot to root ratio (Fageria, 2002b; Foth, 1962; Gupta and Kovács, 1974; Huber et al., 1989; Piper and Weiss, 1993). Others were calculated by simply dividing RB by shoot biomass (Fageria, 2002a; Handa et al., 1985; King and Greer, 1986; Lafitte and Edmeades, 1994; Maizlish et al., 1980; Mengel and Barber, 1974; Merckx et al., 1986, 1987; Todorovic et al., 2001; Tollenaar and Migus, 1984). This method was also used for Karunatilake et al. (2000) and Thom and Watkin (1978), however, biomass data that could not be converted to g plant^{-1} is not shown in Table 1. For Hunt et al. (1991), biomass was obtained from published equations and parameters for maize using their ambient CO_2 treatment as input, and these biomass values were then used to calculate R/S. Root/shoot ratio for Imai and Murata (1976) was obtained by dividing % dry root matter by % dry leaf + stem matter (percentages based on total dry matter).

The results listed in Table 1 reveal the wide variation existing in the literature regarding reported root and shoot biomass and the relationship between the growth of these two organs expressed as R/S ratio. This variation is partially dependent on the type of study conducted (i.e., field vs. greenhouse or growth chamber), the genetic potential of the variety grown, environmental conditions under which plants were grown (either those controlled in a growth chamber or those associated with a particular location, season, or planting date), the method of processing root material after sampling, and the various treatments imposed in the studies. Another potential source of variation is the pattern of root sampling, that is, both the depth and spatial pattern in which roots were collected. As discussed previously in the section on maize root distribution, maize roots are not distributed uniformly throughout the plant population, so a sampling pattern must be established that will reflect the actual root distribution. In addition, a depth of sampling must be chosen that will capture the majority of the roots distributed throughout the soil profile. It was not possible to evaluate the methods of root sampling for each of the studies listed, and it is assumed that in each case, an effort was made to accurately sample the root system. Nevertheless, variations in sampling pattern may have contributed to the variation in reported values. In addition, variations in root washing

technique, particularly in the sieve mesh size chosen (i.e., Livesley et al., 1999), may contribute to variations in reported maize RB.

Table 2 summarizes the average percentage of change in R/S and RB in response to various stress treatments imposed in studies listed in Table 1. These are averages of all sampling dates in which the treatment was imposed, with the exception of population density (Ma et al., 2003), which did not exhibit an effect until the V8 sampling. Table 2 illustrates the plasticity of R/S in response to varying levels of induced stress. A general principle of the functional equilibrium that exists between roots and shoots is that when growth is limited by an essential substance absorbed by the roots, root growth is favored, while shoot growth is favored if the limiting substance is absorbed by the shoots (Brouwer, 1983). For agricultural crops, nutrients are generally the most important substances controlling dry matter distribution in the plant (Brouwer, 1962), and a wide variety of plants are known to increase their R/S in response to decreased soil fertility (Reynolds and D'Antonio, 1996). For the studies summarized in Table 2, nutrient deprivation or deficiency generally resulted in an increase in the overall R/S. Although fewer studies address other stress factors, those listed in Table 2 suggest that water stress, high population, shading, and soil compaction lead to a decrease in R/S. All stress factors listed in Table 2 tend to decrease RB.

The data in Table 1 were used to generate curves of RB (Fig. 1) and R/S (Fig. 2) versus DAE. Before generating the curves, data resulting from treatments that would not reflect common growing practices or field conditions and were intended to manipulate RB and/or R/S for investigative purposes were eliminated from this analysis. Specifically, the data eliminated were the 0 N treatments (Anderson, 1988; Bonifas et al., 2005; Eghball and Maranville, 1993; Feil et al., 1990; Huber et al., 1989; Maizlish et al., 1980; Thom and Watkin, 1978), the 0 P treatments (Fageria and Balinger, 1997; Mollier and Pellerin, 1999), the 0 micronutrient treatments (Fageria, 2002b), the shade treatment (Hébert et al., 2001), and the parasitized treatment (Taylor et al., 1996). Therefore, the curves generated are for plants that are relatively healthy and receive some level of necessary nutrients as well as sufficient light for proper growth. We have, however, retained all data from the two studies in which some level of water stress was applied (Durieux et al., 1994; King and Greer, 1986; Kondo et al., 2000). Several assumptions were made in the generation of these curves. It was assumed that RB and R/S measurements made in the greenhouse and growth chamber adequately reflect those that would be made in the field under comparable conditions, and that experimental effects inherent in these studies would not be great enough to warrant eliminating them from the analysis. Indeed, the plotted data indicate that, except for enhanced R/S early in the season in several non-field studies, results of all three types of studies fall within a similar range and could be analyzed together. The necessity of placing all RB and R/S data on the same time scale also required that we make certain assumptions. Days after emergence was chosen as the time scale, and for curve-fitting purposes, the maize plants in all the studies listed in

Table 2. Average percentage of change over study period in R/S and RB in response to various stress factors as summarized from data shown in Table 1. Values in parentheses are standard errors.

Stress	Change in R/S	Change in RB
	%	
N deficiency	41.6† (8.6)	−6.5‡ (11.5)
P deficiency	121.2§ (64.8)	−11.5§ (31.7)
Water stress	−17.4¶ (n/a)	−44.2# (8.9)
High population	−19.5†† (0.8)	−30.1†† (0.1)
Shading	−42.3‡‡ (9.i)	−56.1‡‡ (5.8)
Soil compaction	−13.3§§ (8.6)	−29.9§§ (5.7)

† Anderson (1988), Bonifas et al. (2005), Eghball and Maranville (1993), Feil et al. (1990), Hocking and Meyer (1991), Huber et al. (1989), Lafitte and Edmeades (1994), Maizlish et al. (1980), Merckx et al. (1987), Thom and Watkin (1977).
‡ Anderson (1988), Eghball and Maranville (1993), Feil et al. (1990), Hocking and Meyer (1991), Lafitte and Edmeades (1994), Maizlish et al. (1980), Merckx et al. (1987), Thom and Watkin (1977).
§ Fageria and Balingar (1997), Mollier and Pellerin (1999), Stryker et al. (1974).
¶ King and Greer (1986).
# Durieux et al. (1994), King and Greer (1986).
†† Ma et al. (2003). V6 data not included.
‡‡ Hébert et al. (2001).
§§ Tubeileh et al. (2003).

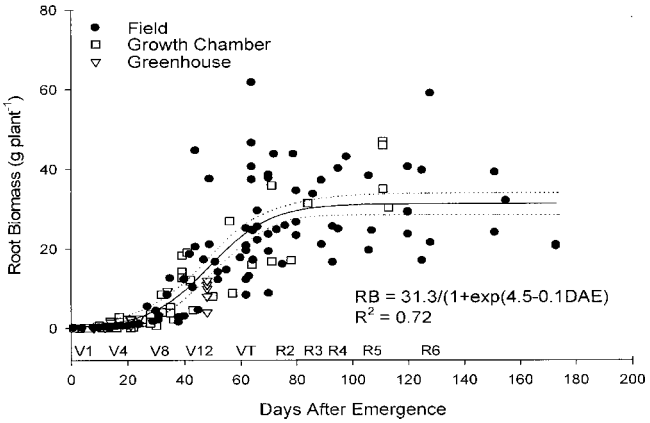

Fig. 1. Maize root biomass vs. days after emergence. Growth stages on the *x*-axis are those reported or estimated from Ritchie et al. (1997). Confidence intervals (95%) for the regression are shown as dotted lines.

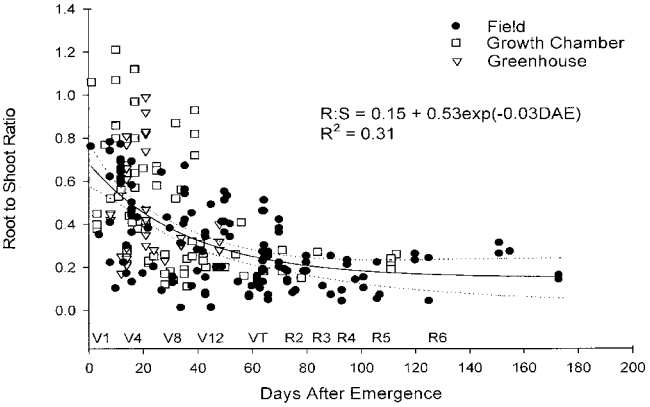

Fig. 2. Maize root/shoot ratio vs. days after emergence. Growth stages on the X-axis are those reported or estimated from Ritchie et al. (1997). Confidence intervals (95%) for the regression are shown as dotted lines.

Table 1 were assumed to conform to the phenological benchmarks outlined by Ritchie et al. (1997) for a typical maize plant. In reality, the length of time between growth stages is dependent on hybrid, temperature, and environmental stresses that may lengthen or shorten the time between vegetative and reproductive stages as reported by Ritchie et al. (1997). However, to place all data on a DAE basis, it was assumed that variations in phenological development were not great enough to limit the analysis only to those studies in which time of sampling is specified as DAE.

A sigmoid curve of the form RB = a/[1+exp(b − c × DAE)], in which RB approaches (a) as DAE increases, was fit to the RB versus DAE data (Fig. 1). The coefficients were significant with P values < 0.0001 and standard errors of the coefficients were 1.4, 0.56, and 0.01 for parameters a, b, and c, respectively. Early in the season, from emergence to around V6, there is very little variation in RB among the various studies and the data closely fit the curve. During this initial phase of growth, the plants accumulate dry matter slowly and differences in experimental conditions and varieties among and within the studies did not greatly influence measured RB. During the linear phase of growth (approximately V8 to VT), growth is much more rapid, and variations in genetic potential, temperature, light, growth medium, moisture level, and measurement technique express themselves as variations in RB. The variation in reported biomass is even greater during the reproductive stages (VT to R6) when maize plants have achieved their maximum RB. Maximum reported RB occurred at the onset of anthesis and the range of values varied between 9 and 65 g plant^{-1}. The average maximum RB predicted by the equation fit to the data in Fig. 1 was ~31 g plant^{-1}. The average C content of coarse and fine maize roots for samples collected during 12 site-years averaged 43.8% of dry matter (D. Walters, unpublished data, 2004), indicating that on a per plant basis, approximately 13.6 g of C is contributed to the soil at harvest by way of standing RB. This maize root C content is slightly higher than the 40% value assumed by Bolinder et al. (1999) and the 42% value assumed by Wilts et al. (2004).

Figure 2 shows R/S ratio vs. DAE fitted to an exponential decay curve of the form [$a + b \times \exp(-k \times$ DAE)] where ($a + b$) gives the initial R/S at emergence and R/S approaches (a) as DAE increases. Coefficients of this equation were significant with P values of 0.007 for a, <0.0001 for b, and 0.0009 for k, and standard errors of the coefficients were 0.05 for a, 0.05 for b, and 0.008 for k. There is a great deal of scatter in the data throughout the growing season as variations in experimental conditions and measurement techniques within and among the studies caused variation in R/S, particularly in the first half of the season (emergence to VT). While results of all three study types for the most part fall within a similar range, growth chamber and greenhouse experiments are more likely to result in a higher R/S values for younger plants. Despite the variation in the results from these 45 studies, a generalized pattern of R/S versus DAE emerged. Root/shoot ratio for 24-d-old plants calculated with our equation (0.41) is only slightly higher than the average R/S (0.37) for three N treatments predicted by Spek and Van Oijen's model (1988). Figure 2 indicates that predicted R/S declined with plant age from a maximum R/S = 0.68 at emergence to a minimum R/S of 0.16 at physiological maturity (128 DAE). Our maturity R/S value is slightly lower than the average R/S of 0.19 reported by Bolinder et al. (1999) for 11 published studies, at least 4 of which reported R/S at a growth stage somewhat before physiological maturity. To test if our values for RB and R/S were reasonable, we estimated the grain dry matter yield that would result given a range in both plant population and harvest index (HI = grain biomass/total aboveground biomass) with an average RB = 31 g plant^{-1} and a final R/S = 0.16 as estimated in Fig. 1 and 2. To make this calculation, we also assumed a cob/stover ratio of 0.15 (D. Walters, unpublished data, 2004). For a maize population of 40 000 plants ha^{-1} and a HI of 0.5 and 0.35, predicted grain dry matter would be 8.9 and 4.8 Mg ha^{-1}, respectively. At a higher plant population (70 000 plants ha^{-1}) with equivalent HI values, predicted dry matter was 15.6 and 8.4 Mg ha^{-1}, respectively. Although the data of Ma et al. (2003) would suggest that the estimate of 31 g plant^{-1} might be too high for the latter population estimate, we did not find any relationship between plant population and estimated RB in the body of data listed in Table 1 (analysis not shown). These are not unrealistic maize production values and suggest that the average values for RB and R/S predicted in Fig. 1 and 2 provide reasonable estimates of standing RB and resulting R/S. At physiological maturity, variation in RB was greater than that for R/S and so suggests that estimates of standing RB are best made as a function of the product of R/S ratio and stover biomass rather than plant population and average RB.

RHIZODEPOSITION

Measurements of RB do not account for all of the belowground allocation of photosynthetic production by the plant. In addition to its use in building biomass, some of the C translocated belowground is used for root respiration, while another portion is transferred to the soil in the form of root turnover, root cap mucigel, and organic exudates. A portion of these root-derived carbohydrates are oxidized to CO_2 by the microbial biomass, ultimately appearing as a component of soil surface CO_2 flux (Arkebauer, 1994). The process by which living roots release organic C into the soil is referred to as rhizodeposition (Kuzyakov and Domanski, 2000). In this paper, we are concerned with *net* rhizodeposited C (i.e., total rhizodeposited C minus the portion respired by rhizosphere heterotrophs) present as soil microbial biomass and soil residue at the time of sampling. We will express this quantity as a percentage of total net root-derived belowground C at time of sampling (i.e., standing RB C + rhizodeposited soil C). We will refer to this value as percentage of net rhizodeposited C (%NRC), and calculate it as follows:

$$\%\mathrm{NRC} = \frac{\mathrm{RDC_{mb}} + \mathrm{RDC_{sr}}}{\mathrm{RBC} + \mathrm{RDC_{mb}} + \mathrm{RDC_{sr}}} \qquad [1]$$

in which RDC_{mb} = rhizodeposited C present in soil microbial biomass at time of sampling, RDC_{sr} = rhizodeposited C present as soil residue at time of sampling, and RBC = C present in standing RB at time of sampling.

Estimates of belowground C inputs rarely include net C rhizodeposited during the growing season. Belowground C contributed by the growing crop may therefore be greatly underestimated and rhizodeposits remaining in the soil at the end of the growing season may be as great as the RB (Flessa et al., 2000). When rhizodeposition is considered in estimates of belowground C deposition, it is often assumed that there is a quantity of rhizodeposited C in the soil equal to RB C at harvest (Bolinder et al., 1999).

Table 3 summarizes the results of twelve maize studies and reports net rhizodeposited C as a percentage of total net belowground root-derived C at various times of sampling (%NRC). The criteria for inclusion in this table was that the studies be non-axenic and that a quantitative measure of rhizodeposition was reported such that %NRC could be calculated. The %NRC values in Table 3 range from a low of 5.2% to a high of 61.8%, with an overall average of 28.6% and a median of 27.7%. Of the nine studies in which sampling was conducted on multiple days, six show a decrease in %NRC over time, two show an increase, while one study showed no temporal pattern. However, due to the wide study to study variation in reported values, as well as the smaller number of data points available, it was not possible to construct a DAE-based curve as we have done previously for RB and R/S. We will, however, address the possible sources of the observed variation in %NRC in maize and make some general conclusions regarding this value.

There is some indication that the environmental conditions under which maize plants are grown will affect %NRC. The studies summarized in Table 3 fall into three types: field, greenhouse (or growth chamber within greenhouse) plus additional lighting, and growth chamber experiments in which all light supplied is artificial. The values of %NRC derived from the field studies ranged from 37.2 to 48.0% with an average of 43.6% (±1.9%, standard error), those from greenhouse plus additional lighting studies ranged from 24.0 to 35.0% with an average of 29.1% (±1.5), and those from growth chamber studies ranged from 5.2 to 61.8% with an average of 22.4% (±4.8). Although it is difficult to make a conclusion based on the small number of studies available, these ranges and averages suggest that exposure to natural sunlight results in higher %NRC, and that the amount of rhizodeposited C measured in studies using only artificial light is highly variable and perhaps more

Table 3. Net rhizodeposited C (present as soil microbial biomass and as soil residue) as a percentage of total net root-derived belowground C (i.e., standing root biomass C + rhizodeposited soil C).

Reference	Study type	Day/night temp	Photoperiod	PPFD	Method	Time of sampling†	NRC
		°C	h	μmol m^{-2} s^{-1}			%
Balesdent and Balabane, 1992	field	–	–	–	^{13}C natural abundance	112 DAP	48.0
						180 DAP	45.4
Cheshire and Mundie, 1990	growth chamber within greenhouse + additional lighting	18/18	16	–	continuous ^{14}C labeling	36 DAG	32.2‡
Helal and Sauerbeck, 1986	growth chamber	24/14	14	392	continuous ^{14}C labeling	30 DAG	10.2
Helal and Sauerbeck, 1989	growth chamber	–	–	–	continuous ^{14}C labeling	21 DAG	13.7
Hétier et al., 1986	growth chamber	–	–	–	continuous ^{14}C labeling	92 DAP	14.1§
Kisselle et al., 2001	field	–	–	–	pulse ^{14}C labeling	3 DAL¶	45.5§
						13 DAL	42.1
						55 DAL	37.2
Martens, 1990	growth chamber within greenhouse + additional lighting	22/15	14	180-400	continuous ^{14}C labeling	46 DAP	27.0
						76 DAP	28.4
						111 DAP	35.0
Merckx et al., 1986	growth chamber	21/16	16	314	continuous ^{14}C labeling	28 DAG	11.6
						42 DAG	5.2
Merckx et al., 1987	growth chamber	–	–	–	continuous ^{14}C labeling	28 DAG	7.7
						35 DAG	9.1
						42 DAG	13.7
Qian et al., 1997	greenhouse + additional lighting	27/21	14	180-400	^{13}C natural abundance	28 DAE	34.3
						56 DAE	26.6
						84 DAE	24.0
						112 DAE	25.5
Tubeileh et al., 2003	growth chamber	23/18	16	300-400	pulse ^{14}C labeling	21 DAP	34.8#
						35 DAP	26.5
						42 DAP	42.2
Whipps, 1985	growth chamber	18/14	16	350	continuous ^{14}C labeling	14 DAT††	61.8
						28 DAT	41.1

† DAG, days after germination; DAP, days after planting; DAE, days after emergence; DAT, days after transplanting; DAL, days after ^{14}C pulse labeling.
‡ Based on the authors' estimate that 4/5 of their soluble fraction was induced root lysate.
§ Averaged across treatments.
¶ Pulse labeling carried out 10-12 July.
# Only data for non-compacted soil treatment shown.
†† Dry weight of seedlings at transplanting = 280 ± 7 mg.

dependent on both quantity and quality of light supplied. The maximum photosynthetic photon flux density (PPFD) reported in the controlled studies listed in Table 3 (both greenhouse and growth chamber) is 400 μmol m^{-2} s^{-1}, which would be considered a moderate PPFD (Nobel, 1991). As a comparison, measured PPFD between 0530 and 1930 h DST in a maize field near Mead, NE during June, July, and August of 2001 ranged from 0.5 to 2013 μmol m^{-2} s^{-2}, and the average of all hourly PPFD measurements during this time period was 838 μmol m^{-2} s^{-2}. Hodge et al. (1997) found that for *Lolium perenne* seedlings grown at a constant 20°C, the total amount of C released from the roots during a 3-h chase period following $^{14}CO_2$ labeling was significantly greater from seedlings grown under a PPFD of 1000 μmol m^{-2} s^{-1} than under 350 μmol m^{-2} s^{-1}, although alteration in C allocation expressed as a percentage of total plant C did not occur. The leaves of C_4 species such as maize show a virtually linear increase in CO_2 uptake rate with increasing level of irradiance (Rosenberg et al., 1983). Maize leaves exposed to full sun during growth may still not reach light saturation even at a PPFD of 2000 μmol m^{-2} s^{-1}, which corresponds to full sunlight (Norman and Arkebauer, 1991). However, in the case of a plant adapted to full sun that has been grown under shaded conditions at a lower PPFD, photosynthesis saturates at a lower PPFD, indicating that the photosynthetic properties of a leaf depend on its previous growing conditions (Taiz and Zeiger, 2002). It is therefore possible that the leaves of maize plants growing in the field and exposed to full sunlight have a greater photosynthetic capacity, and therefore a greater potential to exude excess C from the root system, than plants growing under the lower irradiance levels of controlled conditions.

Another potential source of variation in %NRC from these studies is the range of different temperature regimes under which maize plants were grown. Air temperature, through its effect on soil temperature, is likely to affect the rate at which rhizodeposited C is respired by rhizosphere heterotrophs. Mean annual air temperature is the single best predictor of the annual soil respiration rate of a specific ecosystem (Raich and Schlesinger, 1992). Davidson et al. (1998) reported that an exponential model based on soil temperature accounted for 80% of the variation in the soil surface CO_2 fluxes in a hardwood forest.

It is therefore possible that %NRC is at least partially a function of PPFD, with increasing irradiance levels and photoperiod leading to increased photosynthesis, as well as of soil temperature, with increasing temperature leading to higher soil respiration rates and therefore a lower %NRC. Although a small number of controlled studies is shown in Table 3 for which temperature, PPFD, and photoperiod are reported, a convincing pattern emerges when %NRC is plotted against the maximum reported experimental photosynthetically active radiation (PAR) in moles per square meter per day divided by average air temperature (Fig. 3). For this analysis, maximum PAR values were calculated by multiplying the maximum reported PPFD by the time in the

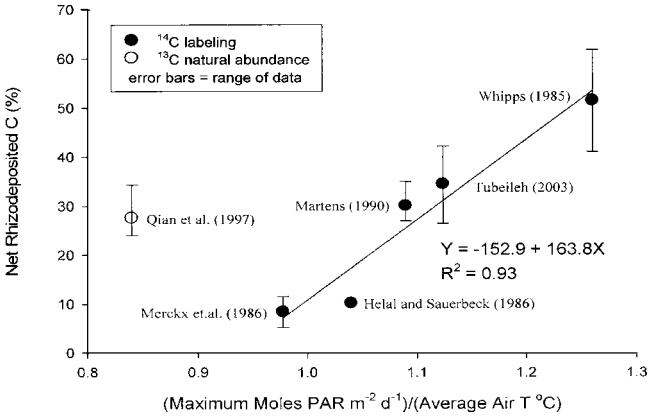

Fig. 3. Net rhizodeposited C expressed as a percentage of total net root-derived C plotted against the quotient of maximum daily photosynthetically active radiation (PAR) and average air temperature.

reported photoperiod. Maximum reported PPFD was used because for those studies reporting a range of PPFD, this range had different meanings, and it would be difficult to determine an average PPFD based on available information. The range reported by Tubeileh et al. (2003) represents a spatial range within the growth cabinet, with plants rotated daily to provide equal exposure to maximum PPFD levels (Ashraf Tubeileh, personal communication, 2005). In the greenhouse experiment described by Qian et al. (1997), the range reported is a target range, in which the additional light source was intended to compensate for low light conditions (Qian, 1995). Average air temperature was used since soil temperature was not reported in these studies, and was calculated as the average of reported day and night temperatures without adjustment for photoperiod. A surprisingly high R^2 of 0.93 resulted from linear regression through the data representing the mean %NRC values from the ^{14}C labeling controlled studies. Note that the ^{14}C data are from five separate and independent studies reported between 1986 and 2003. However, Fig. 3 is not intended to represent a functional relationship, nor should it be interpreted as a method of predicting %NRC from inputs of PPFD and temperature. Figure 3 does, however, suggest that such a functional relationship might be established by experiments in which PPFD and temperature are varied in such a way as to reflect field conditions. The single study by Qian et al. (1997) does not fall along this line and this is the only study of the six that are plotted in Fig. 3 that used changes in the δ^{13}C of maize soil to estimate %NRC. The lack of congruence with the other ^{14}C studies is probably due to a much lower sensitivity of δ^{13}C as a quantitative C tracer compared with ^{14}C. The relationship between %NRC and the ratio of maximum daily PAR to average air temperature exhibited by the ^{14}C controlled studies, suggests that the specific irradiance and temperature regimes imposed may partially explain the wide range of %NRC reported in these studies. As ambient temperature increases with a corresponding increase in soil temperature, the rate of heterotrophic respiration of rhizodeposited C apparently increases resulting in lower %NRC. Conversely, an

increase in photoperiod and PPFD results in a greater %NRC as seen in Fig. 3. This relationship also suggests that %NRC as a portion of NPP may vary quite widely with latitude and its influence on PAR and microbial activity. For estimating net rhizodeposited maize C based on measurements or estimates of standing RB in field studies, an average of the results of the two field studies in Table 3, %NRC ~44 ± 2%, may be more realistic than applying the overall average of all studies. However, more such field studies are needed, particularly those that investigate the relationship between net rhizodeposition, environmental conditions, and plant phenology.

If we assume that the C content of rhizodeposited material is similar to that of RB, then average belowground maize C deposition at physiological maturity might be estimated from aboveground vegetative (stover) dry matter. A field value of 44 ± 2% NRC combined with an estimated R/S ratio of 0.16 ± 0.07 at physiological maturity gives a (RB + net rhizodeposition)/shoot ratio of 0.29 = [0.16/(1–0.44)] at physiological maturity with a range of ~ ± 0.13%. Our value is much lower than values of 1.8 to 3.5 estimated in several recent $\delta^{13}C$ studies in long-term continuous maize sites that had been subject to stover harvest or stover incorporation (Allmaras et al., 2004; Wilts et al., 2004). However, it is unlikely that these estimates are realistic as they represent maize assimilatory capacities and efficiencies far in excess of measured values (Penning de Vries et al., 1974; Loomis and Amthor, 1999; Lindquist et al., 2005).

CONCLUSIONS

There exists a relatively small body of literature that reports measured values of maize RB and R/S and even fewer articles that provide measurement throughout the life cycle of the maize plant. Significant variation in reported values of maize RB and R/S are due to the variety of measurement techniques employed, spatial variability in maize root distribution, and the errors inherent in scaling point measurements (such as soil coring) to whole plant values. Root/shoot ratio is a simple, straight forward parameter that can be used to estimate C allocation to the root when aboveground shoot yield (leaf + stem) is known. In this study, the results of 45 maize root studies that spanned the entire life cycle of the maize plant were assembled and analyzed with RB and R/S values plotted verses DAE. Average maize R/S varied from 0.68 at emergence to 0.16 at physiological maturity. Maximum RB occurred just after anthesis with an average RB of 31 g plant^{-1}. In addition to maize RB C, net rhizodeposited C must also be considered when estimating the total contribution of maize roots to SOC. A great variation in %NRC exists in the literature and we calculated an average reported value for %NRC of 29%, however the range reported in the literature varied from 5 to 62%. This variation is most likely due to the environmental conditions under which individual experiments are conducted (e.g., PAR and soil temperature). A very high correlation between %NRC and the ratio PAR/Average Air Temperature ($R^2 = 0.93$) from a family of independent studies implies that the rate of photosynthesis, combined with soil heterotrophic activity, affects the actual amount of net rhizodeposited C during the growing season. Based on these analyses, and assuming that C content of root and shoot material is similar, we conclude that, on average, the net belowground C deposition at maize physiological maturity might be estimated as 29 ± 13% of shoot biomass C for maize that has not experienced stress. Considerable plasticity, however, is apparent in maize R/S in response to various stress factors. Quantitative data regarding the physiological and environmental factors influencing extent of rhizodeposited C by maize is rare and further field studies are needed to characterize maize rhizodeposition throughout the growing season.

ACKNOWLEDGMENTS

This material is based on the work supported by the U.S. Department of Energy, Office of Science, Biological and Environmental Research Program (BER), Grant No. DE-FG02-03ER63639; and by the Cooperative State Research, Education and Extension Service, U.S. Department of Agriculture, under Agreement No. 2001-38700-11092.

REFERENCES

Aina, P.O., and H.O. Fapohunda. 1986. Root distribution and water uptake patterns of maize cultivars field-grown under differential irrigation. Plant Soil 94:257–265.

Allmaras, R.R., D.R. Linden, and C.E. Clapp. 2004. Corn-residue transformations into root and soil carbon as related to nitrogen, tillage and stover management. Soil Sci. Soc. Am. J. 68:1366–1375.

Allmaras, R.R., W.W. Nelson, and W.B. Voorhees. 1975. Soybean and corn rooting in southwestern Minnesota: II. Root distributions and related water inflow. Soil Sci. Soc. Am. Proc. 39:771–777.

Anderson, E.L. 1988. Tillage and N fertilization effects on maize root growth and root:shoot ratio. Plant Soil 108:245–251.

Arkebauer, T.J. 1994. Plant physiology in relation to fluxes of carbon dioxide and water vapor. p. 33–43. *In* J.F. Griffiths (ed.) Handbook of agricultural meteorology. Oxford Univ. Press, New York.

Balesdent, J., and M. Balabane. 1992. Maize root-derived soil organic carbon estimated by natural ^{13}C abundance. Soil Biol. Biochem. 24:97–101.

Balesdent, J., and M. Balabane. 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. Soil Biol. Biochem. 28:1261–1263.

Balesdent, J., and A. Mariotti. 1996. Measurement of soil organic matter turnover using ^{13}C natural abundance. p. 83–111, *In* T.W. Boutton and S. Yamasaki (ed.) Mass spectrometry of soils. Marcel Dekker, Inc., New York.

Böhm, W. 1979. Methods of studying root systems. Springer-Verlag, Berlin.

Bolinder, M.A., D.A. Angers, M. Giroux, and M.R. Laverdière. 1999. Estimating C inputs retained as soil organic matter from corn (*Zea Mays* L.). Plant Soil 215:85–91.

Bonifas, K.D., D.T. Walters, K.G. Cassman, and J.L. Lindquist. 2005. Nitrogen supply affects root:shoot ratio in corn and velvetleaf (Abutilon theophrasti). Weed Sci. 53:670–675.

Boutton, T.W. 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. p. 47–82. *In* T.W. Boutton and S. Yamasaki (ed.) Mass spectrometry of soils. Marcel Dekker, Inc., New York.

Brouwer, R. 1962. Nutritive influences on the distribution of dry matter in the plant. Neth. J. Agric Sci. 10:399–408.

Brouwer, R. 1983. Functional equilibrium: Sense or nonsense? Neth. J. Agric. Sci. 31:335–348.

Buman, R.A., T.E. Schumacher, and W.E. Riedell. 1994. Modified soil monolith technique for characterizing root systems. Crop Sci. 34: 296–299.

Buyanovsky, G.A., and G.H. Wagner. 1986. Post-harvest residue input to cropland. Plant Soil 93:57–65.

Cheshire, M.V., and C.M. Mundie. 1990. Organic matter contributed to soil by plant roots during growth and decomposition of maize. Plant Soil 121:107–114.

Crozier, C.R., and L.D. King. 1993. Corn root dry matter and nitrogen distribution as determined by sampling multiple soil cores around individual plants. Commun. Soil Sci. Plant Anal. 24:1127–1138.

Davidson, E.A., E. Belk, and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob. Change Biol. 4:217–227.

Durieux, R.P., E.J. Kamprath, W.A. Jackson, and R.H. Moll. 1994. Root distribution of corn: The effect of nitrogen fertilization. Agron. J. 86:958–962.

Dwyer, L.M., B.L. Ma, D.W. Stewart, H.N. Hayhoe, D. Balchin, J.L.B. Culley, and M. McGovern. 1996. Root mass distribution under conventional and conservation tillage. Can. J. Soil Sci. 76:23–28.

Eghball, B., and J.W. Maranville. 1993. Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stresses. Agron. J. 85:147–152.

Engels, C. 1993. Differences between maize and wheat in growth-related nutrient demand and uptake of potassium and phosphorus at suboptimal root zone temperatures. Plant Soil 150:129–138.

Ewel, J., F. Benedict, C. Berish, B. Brown, S. Gliessman, M. Amador, R. Bermúdez, A. Martínez, R. Miranda, and N. Price. 1982. Leaf area, light transmission, roots and leaf damage in nine tropical plant communities. Agro-Ecosystems 7:305–326.

Fageria, N.K. 2002a. Dry matter yield of common bean, lowland rice, corn, soybean, and wheat at different basic cation saturation ratios in acid soil. Commun. Soil Sci. Plant Anal. 33:519–531.

Fageria, N.K. 2002b. Micronutrients' influence on root growth of upland rice, common bean, corn, wheat, and soybean. J. Plant Nutr. 25:613–622.

Fageria, N.K., and V.C. Baligar. 1997. Phosporus-use efficiency by corn genotypes. J. Plant Nutr. 20:1267–1277.

Farquhar, G.D., J.R. Ehleringer, and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40:503–537.

Feil, B., R. Thiraporn, G. Geisler, and P. Stamp. 1990. Root traits of maize seedlings– indicators of nitrogen efficiency? Plant Soil 123:155–159.

Flessa, H., B. Ludwig, B. Heil, and W. Merbach. 2000. The origin of soil organic C, dissolved organic C and respiration in a long-term maize experiment in Halle, Germany, determined by ^{13}C natural abundance. J. Plant Nutr. Soil Sci. 163:157–163.

Food and Agricultural Organization. 2002. Production Yearbook, 2001. FAO, Rome.

Foth, H.D. 1962. Root and top growth of corn. Agron. J. 54:49–52.

Gajri, P.R., V.K. Arora, and K. Kumar. 1994. A procedure for determining average root length density in row crops by single-site augering. Plant Soil 160:41–47.

Gale, W.J., and C.A. Cambardella. 2000. Carbon dynamics of surface residue- and root-derived organic matter under simulated no-till. Soil Sci. Soc. Am. J. 64:190–195.

Gerwitz, A., and E.R. Page. 1974. An empirical mathematical model to describe plant root systems. J. Appl. Ecol. 11:773–781.

Grant, R.F. 1989. Simulation of carbon assimilation and partitioning in maize. Agron. J. 81:563–571.

Gupta, D. and I. Kovács. 1974. Root characters and their relationships with yield of *Opaque*-2 and analogous normal maize single, 3-way and double cross hybrids and inbred lines. Z. Acker- Pflanzenbau 139:233–241.

Handa, S., D.M. Huber, H.L. Warren, and C.Y. Tsai. 1985. Nitrogen nutrition and N- assimilation in maize seedlings. Can. J. Plant Sci. 65:87–93.

Hayhoe, H. 1981. Analysis of a diffusion model for plant root growth and an application to plant soil-water uptake. Soil Sci. 131:334–343.

Hébert, Y., E. Guingo, and O. Loudet. 2001. The response of root/shoot partitioning and root morphology to light reduction in maize genotypes. Crop Sci. 41:363–371.

Helal, H.M., and D. Sauerbeck. 1986. Effect of plant roots on carbon metabolism of soil microbial biomass. Z. Pflanzenernaehr. Bodenkd. 149:181–188.

Helal, H.M., and D. Sauerbeck. 1989. Carbon turnover in the rhizosphere. Z. Pflanzenernähr. Bodenk. 152:211–216.

Hétier, J.M., F. Andreux, E. Schouller, and C. Marol. 1986. Organic matter inputs to soil after growth of carbon-14-nitrogen-15 labeled maize. Soil Sci. Soc. Am. J. 50:76–80.

Hocking, P.J., and C.P. Meyer. 1991. Effects of CO_2 enrichment and nitrogen stress on growth, and partitioning of dry matter and nitrogen in wheat and maize. Aust. J. Plant Physiol. 18:339–356.

Hodge, A., E. Paterson, B. Thornton, P. Millard, and K. Killham. 1997. Effect of photon flux density on carbon partitioning and rhizosphere carbon flow of *Lolium perenne*. J. Exp. Bot. 48:1797–1805.

Huber, S.C., T. Sugiyama, and R.S. Alberte. 1989. Photosynthetic determinants of growth in maize plants: Effects of nitrogen nutrition on growth, carbon fixation and photochemical features. Plant Cell Physiol. 30:1063–1072.

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1991. Response to CO_2 enrichment in 27 herbaceous species. Funct. Ecol. 5:410–421.

Imai, K., and Y. Murata. 1976. Effect of carbon dioxide concentration on growth and dry matter production in crop plants. Proc. Crop Sci. Soc. Jpn. 45:598–606.

Jones, C.A., W.L. Bland, J.T. Ritchie, and J.R. Williams. 1991. Simulation of Root Growth. p. 91–123 *In* J. Hanks and J.T. Ritchie (ed.) Modeling plant and soil systems. ASA, CSSA, and SSSA, Madison, WI.

Jones, C.A., and J.R. Kiniry (ed.). 1986. CERES-Maize: A simulation model of maize growth and development. Texas A&M Univ. Press, College Station, TX.

Karunatilake, U., H.M. van Es, and R.R. Schindelbeck. 2000. Soil and maize response to plow and no-tillage after alfalfa-to-maize conversion on a clay loam soil in New York. Soil Tillage Res. 55: 31–42.

Kaspar, T.C., H.J. Brown, and E.M. Kassmeyer. 1991. Corn root distribution as affected by tillage, wheel traffic, and fertilizer placement. Soil Sci. Soc. Am. J. 55:1390–1394.

King, K.M., and D.H. Greer. 1986. Effects of carbon dioxide enrichment and soil water on maize. Agron. J. 78:515–521.

Kisselle, K.W., C.J. Garrett, S. Fu, P.F. Hendrix, D.A. Crossley, Jr., D.C. Coleman, and R.L. Potter. 2001. Budgets for root-derived C and litter-derived C: Comparison between conventional tillage and no tillage soils. Soil Biol. Biochem. 33:1067–1075.

Kondo, M., M.V.R. Murty, and D.V. Aragones. 2000. Characteristics of root growth and water uptake from soil in upland rice and maize under water stress. Soil Sci. Plant Nutr. 46:721–732.

Kovar, J.L., S.A. Barber, E.J. Kladivko, and D.R. Griffith. 1992. Characterization of soil temperature, water content, and maize root distribution in two tillage systems. Soil Tillage Res. 24:11–27.

Kuzyakov, Y., and G. Domanski. 2000. Carbon input by plants into the soil. Review. J. Plant Nutr. Soil Sci. 163:421–431.

Lafitte, H.R., and G.O. Edmeades. 1994. Improvement for tolerance to low soil nitrogen in tropical maize III. Variation in yield across environments. Field Crops Res. 39:27–38.

Lal, R., J.M. Kimble, R.F. Follett, and C.V. Cole. 1998. The potential of U.S. cropland to sequester carbon and mitigate the greenhouse effect. Ann Arbor Press, Chelsea, MI.

Lindquist, J.L., T.J. Arkebauer, D.T. Walters, K.G. Cassman, and A. Dobermann. 2005. Maize radiation use efficiency under optimal growth conditions. Agron. J. 97:72–78.

Livesley, S.J., C.L. Stacey, P.J. Gregory, and R.J. Buresh. 1999. Sieve size effects on root length and biomass measurements of maize (*Zea mays*) and *Grevillea robusta*. Plant Soil 207:183–193.

Loomis, M.J., and J.S. Amthor. 1999. Yield potential, plant assimilatory capacity and metabolic efficiencies. Crop Sci. 39:1584–1596.

Ma, B.L., L.M. Dwyer, and C. Costa. 2003. Row spacing and fertilizer nitrogen effects on plant growth and grain yield of maize. Can. J. Plant Sci. 83:241–247.

Maizlish, N.A., D.D. Fritton, and W.A. Kendall. 1980. Root morphology and early development of maize at varying levels of nitrogen. Agron. J. 72:25–31.

Martens, R. 1990. Contribution of rhizodeposits to the maintenance and growth of soil microbial biomass. Soil Biol. Biochem. 22: 141–147.

Mengel, D.B., and S.A. Barber. 1974. Development and distribution of the corn root system under field conditions. Agron. J. 66:341–344.

Merckx, R., A. Dijkstra, A. den Hartog, and J.A. van Veen. 1987. Production of root-derived material and associated microbial growth in soil at different nutrient levels. Biol. Fertil. Soils 5:126–132.

Merckx, R., J.H. van Ginkel, J. Sinnaeve, and A. Cremers. 1986. Plant-induced changes in the rhizosphere of maize and wheat. I. Production and turnover of root-derived material in the rhizosphere of maize and wheat. Plant Soil 96:85–93.

Mollier, A., and S. Pellerin. 1999. Maize root system growth and development as influenced by phosphorus deficiency. J. Exp. Bot. 50:487–497.

Nobel, P.S. 1991. Physicochemical and environmental plant physiology. Academic Press, Inc., San Diego, CA.

Norman, J.M., and T.J. Arkebauer. 1991. Predicting canopy photosynthesis and light-use efficiency from leaf characteristics. p. 75–94. *In* K.J. Boote and R.S. Loomis (ed.) Modeling crop photosynthesis–from biochemistry to canopy. CSSA Spec. Publ. 19. CSSA and ASA, Madison, WI.

Oikeh, S.O., J.G. Kling, W.J. Horst, V.O. Chude, and R.J. Carsky. 1999. Growth and distribution of maize roots under nitrogen fertilization in plinthite soil. Field Crops Res. 62:1–13.

Oliveira, M.R.G., M. van Noordwijk, S.R. Gaze, and G. Brouwer. 2000. Auger Sampling, Ingrowth Cores, and Pinboard Methods. p. 175–210 *In* A.L. Smit et al (ed.) Root methods: A handbook. Springer-Verlag, Berlin.

Osaki, M., T. Shinano, M. Matsumoto, J. Ushiki, M.M. Shinano, M. Urayama, and T. Tadano. 1995. Productivity of high-yielding crops. V. Root growth and specific absorption rate of nitrogen. Soil Sci. Plant Nutr. 41:635–647.

Pagès, L., M.O. Jordan, and D. Picard. 1989. A simulation model of the three-dimensional architecture of the maize root system. Plant Soil 119:147–154.

Patterson, D.T., and E.P. Flint. 1980. Potential effects of global atmospheric CO_2 enrichment on the growth and competitiveness of C_3 and C_4 weed and crop plants. Weed Sci. 28:71–75.

Penning de Vries, F.W.T., A.H.M. Brunsting, and H.H. Van Laar. 1974. Products, requirements and efficiency of biosynthesis: A quantitative approach. J. Theor. Biol. 45:339–377.

Piper, E.L., and A. Weiss. 1993. Defoliation during vegetative growth of corn: The shoot:root ratio and yield implications. Field Crops Res. 31:145–153.

Qian, J.H. 1995. Crop plant contributions to root zone available carbon and microbial transformations of nitrogen. Ph.D. diss. Univ. of Nebraska, Lincoln.

Qian, J.H., J.W. Doran, and D.T. Walters. 1997. Maize plant contributions to root zone available carbon and microbial transformations of nitrogen. Soil Biol. Biochem. 29:1451–1462.

Raich, J.W., and W.H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99.

Reynolds, H.L., and C. D'Antonio. 1996. The ecological significance of plasticity in root weight ratio in response to nitrogen: Opinion. Plant Soil 185:75–97.

Richner, W., A. Soldati, and P. Stamp. 1996. Shoot-to-root relations in field-grown maize seedlings. Agron. J. 88:56–61.

Ritchie, S.W., J.J. Hanway, and G.O. Benson. 1997. How a corn plant develops. Spec. Rep. 48. Iowa State University of Science and Technology Cooperative Extension Service, Ames, IA.

Rogers, H.H., G.E. Bingham, J.D. Cure, J.M. Smith, and K.A. Surano. 1983. Responses of selected plant species to elevated carbon dioxide in the field. J. Environ. Qual. 12:569–574.

Rosenberg, N.J., B.L. Blad, and S.B. Verma. 1983. Microclimate: The biological environment. 2nd ed. John Wiley & Sons, New York.

Sionit, N., H. Hellmers, and B.R. Strain. 1982. Interaction of Atmospheric CO_2 enrichment and irradiance on plant growth. Agron. J. 74:721–725.

Spek, L., and M. Van Oijen. 1988. A simulation model of root and shoot growth at different levels of nitrogen availability. Plant Soil 111:191–197.

Stöckle, C.O., M. Donatelli, and R. Nelson. 2003. CropSyst, a cropping systems simulation model. Eur. J. Agron. 18:289–307.

Stryker, R.B., J.W. Gilliam, and W.A. Jackson. 1974. Nonuniform phosphorus distribution in the root zone of corn: Growth and phosphorus uptake. Soil Sci. Soc. Am. Proc. 38:334–340.

Taiz, L., and E. Zeiger. 2002. Plant Physiology. 3rd ed. Sinauer Associates, Inc. Sunderland, MA.

Taylor, A., J. Martin, and W.E. Seel. 1996. Physiology of the parasitic association between maize and witchweed (*Striga hermonthica*): Is ABA involved? J. Exp. Bot. 47:1057–1065.

Thom, E.R., and B.R. Watkin. 1978. Effect of rate and time of fertilizer nitrogen application on total plant, shoot, and root yields of maize (*Zea mays* L.). N.Z. J. Exp. Agric. 6:29–38.

Todorovic, C., C. Nguyen, C. Robin, and A. Guckert. 2001. Root and microbial involvement in the kinetics of ^{14}C-partitioning to rhizosphere respiration after a pulse labeling of maize assimilates. Plant and Soil 228:179–189.

Tollenaar, M., and W. Migus. 1984. Dry matter accumulation of maize grown hydroponically under controlled-environment and field conditions. Can. J. Plant Sci. 64:475–485.

Tubeileh, A., V. Groleau-Renaud, S. Plantureaux, and A. Guckert. 2003. Effect of soil compaction on photosynthesis and carbon partitioning within a maize-soil system. Soil Tillage Res. 71: 151–161.

U.S. Census Bureau. 2002. Statistical abstract of the United States: 2002. U.S. Census Bureau. Washington, DC.

Verma, S.B., A. Dobermann, K.G. Cassman, D.T. Walters, J.M. Knops, T.J. Arkebauer, A.E. Suyker, G.G. Burba, B. Amos, H. Yang, D. Ginting, K.G. Hubbard, A.A. Gitelson, and E.A. Walter-Shea. 2005. Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. Agric. For. Meteorol. 131:77–96.

Warncke, D.D., and S.A. Barber. 1974. Root development and nutrient uptake by corn grown in solution culture. Agron. J. 66:514–516.

Whipps, J.M. 1985. Effect of CO_2 concentration on growth, carbon distribution and loss of carbon from the roots of maize. J. Exp. Bot. 36:644–651.

Wilts, A.R., D.C. Reicosky, R.R. Allmaras, and C.E. Clapp. 2004. Long-term corn residue effects: Harvest alternatives, soil carbon turnover, and root-derived carbon. Soil Sci. Soc. Am. J. 68:1342–1351.

Yang, H.S., A. Dobermann, J.L. Lindquist, D.T. Walters, T. Arkebauer, and K.G. Cassman. 2004. Hybrid-Maize– a maize simulation model that combines two crop modeling approaches. Field Crops Res. 87:131–154.