Relationships between Root Size and Postharvest Respiration Rate

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ABSTRACT

Sugarbeet (*Beta vulgaris* L.) root size has been implicated as a factor influencing storage respiration rate, yet the relationship between root size and respiration is unclear. Sugarbeet root size is dependent on cultural, environmental, and genetic factors and can vary significantly within and between fields. To evaluate the effect of root size on respiration rate and explore the morphological mechanisms that regulate respiration in sugarbeet roots, the relationships of respiration rate and total root respiration with root mass, surface area, and the ratio of surface area to mass (specific surface area) were determined using three field-grown varieties. Respiration rates for the sugarbeet varieties KW 2249, VDH 46177, and Beta 4818 were associated with root mass (R^2 = 0.55, 0.40, and 0.47), surface area (R^2 = 0.38, 0.29, and 0.39), and specific surface area (R^2 = 0.57, 0.34, and 0.36) by sigmoidal relationships. For each variety, there was a critical root size above which size had little impact on respiration rate. Below this critical size, root respiration rate increased substantially as root mass or surface area decreased. This critical beet size was 0.68, 0.50, and 0.86 kg for KW 2249, VDH 46177, and Beta 4818, respectively. Total respiration, i.e. respiration per root, for KW 2249, VDH 46177, and Beta 4818 was directly associated with root mass (R^2 = 0.71, 0.52, and 0.21) and surface area (R^2 = 0.72, 0.46, and 0.11) and inversely related to specific surface area (R^2 = 0.33, 0.29, and 0.15). Root mass rather than surface area or specific

surface area generally provided the best description of the relationships of root size with respiration rate and total root respiration. This contrasts with suppositions from earlier studies that the relationship between respiration and root size is best described by root surface area or specific surface area. The results suggest that storage respiration rates can be adversely affected when small roots are placed into storage piles.

Respiration is the metabolic process that utilizes sugarbeet's sucrose reserves to provide energy and carbon substrates for maintaining healthy tissue, healing wounds from harvest and piling, and defending against pathogens. Postharvest respiration may account for 60 to 80% of sucrose loss during sugarbeet storage (Wyse and Dexter, 1971). Akeson and Widner (1981) and Wyse et al. (1978) reported a high correlation ($r = 0.92$ and 0.90, respectively) between sucrose loss in storage and respiration rate. Although sucrose loss during storage has been correlated with respiration, no correlation between percent sugar content and respiration rate has been found (Wyse et al., 1978).

There are conflicting reports regarding the importance of sugarbeet root size to postharvest respiration rate. Some research has shown that small beets have greater respiration rates than large beets (Stout, 1954; Wyse and Dilley, 1973; Koster et al., 1980). Stout (1954) reported a 23% decrease in respiration rate as beet mass increased from 0.3 to 2.2 kg. However, storage temperature and duration were not reported, and only four beet size classes with average weights of 0.3, 0.5, 1.1 and 2.2 kg were evaluated. Koster et al. (1980) examined respiration from large and small roots obtained by growing plants in rows spaced 12 and 18 cm apart and reported a significant increase in respiration from small roots during 18 days of storage at room temperature. Similarly, Wyse and Dilley (1973) found small roots with an average mass of 0.58 kg respired more rapidly than large roots averaging 1.36 kg when stored at 10 and 20°C. However, no correlation was found between root size and respiration rate among 97 breeding lines stored at 5°C (Wyse et al., 1978).

Sugarbeet root size is dependent upon numerous cultural, environmental, and genetic factors. Variety, soil fertility, disease, insect pressure, and plant population may impact root size (Campbell, 2002; Draycott and Christenson, 2003; Whitney and Duffus, 1995; Khan et al., 2005). Increased root yield may be associated with increased ploidy

level (Campbell, 2002) and soil nitrogen concentration (Draycott and Christenson, 2003). Sugarbeet root maggot and root diseases such as rhizomania and *Aphanomyces* stunt growth and decrease overall root size (Whitney and Duffus, 1995). In a recent field study evaluating row spacing in Minnesota, Khan et al. (2005) reported a 25% reduction in beet mass when row spacing was decreased from 22 to 11 inches.

In studies documenting a relationship between decreasing beet size and elevated respiration, it has been theorized that this relationship is evidence that gas diffusion through the root limits respiration of internal tissues. Respiration rate in storage organs is affected by oxygen and carbon dioxide concentrations (Kays and Paull, 2004). Concentration of oxygen can limit respiration if present in insufficient quantity, while elevated carbon dioxide content can also inhibit respiration. Both Stout (1954) and Koster et al. (1980) concluded that respiration rate was related to surface area per unit weight, or specific surface area, which accounts for both root mass and shape, and provides a more accurate description of the length of the gas diffusion path than mass alone. More recently, Klotz et al. (2003) reported that the respiration rate of root surface tissues was 8-fold higher than that of internal tissues, indicating that respiration rate may be associated with root surface area. Although surface area or specific surface area may influence respiratory activity, neither parameter has been determined in these earlier studies.

The objectives of this study were to define the relationships between respiration and root size, and to use these relationships to improve our understanding of the morphological mechanisms controlling sugarbeet root respiration. To accomplish this, root mass, surface area, specific surface area, and respiration rate were measured on 90 individual roots from each of three varieties, and the relationships between these parameters were determined.

MATERIALS AND METHODS

Sugarbeet roots from three varieties and two locations were used: KW 2249 was harvested from Fargo, ND, and VDH 46177 and Beta 4818 were harvested from Foxhome, MN. Fertilization and weed control were in accord with recommended production guidelines (Khan, 2004). Fungicide for Cercospora leafspot control was applied as needed. KW 2249 was hand harvested on 1 Oct. 2004, and VDH 46177 and Beta 4818 were mechanically harvested on 4 Oct. 2004. Only healthy, regularly shaped roots were used. Roots were hand washed, placed in perforated plastic bags, and stored at 6ºC and 95% relative humidity. Root respiration rates, surface area, and mass were determined after 35

days in storage using 90 roots per variety.

Respiration was measured on individual roots in an open system using a LI-6400 infrared CO_2 gas analyzer (LI-COR, Lincoln, NE) connected to a 7 L container, with an air flow rate of 1000 μmol s^{-1}. Roots were equilibrated for 10 min in the chamber prior to CO_2 measurement.

Surface area was determined by the shrink-wrap replica method described by Furness et al. (2002) with minor modifications. Briefly, shrink-film (Horizon Trading Co., Suffolk, VA) was wrapped around individual roots and shrunk with a heat gun. The shrink-wrapped roots were spray-painted black. Shrink-wrap was removed from the root, cut into strips to allow flattening, and surface area of the shrink-wrap was determined with an AAC-400 leaf area meter (Hayashi Denkoh Co., Tokyo, Japan). Specific surface area was obtained by dividing root surface area by root mass.

SigmaPlot Version 8.0 (SPSS Inc., Chicago, IL) was used to determine the best fit equations for the response variables. A sigmoidal four-parameter equation was used to describe the response of root mass, surface area, and specific surface area with respiration:

$$[\text{Equation 1}] \qquad y = y_0 + \frac{a}{1 + \exp\{-[(x-x_0)/b]\}}$$

Regression procedures outlined by SigmaPlot were used to provide least-squares estimates of the regression coefficients and coefficients of determination with significance defined as $P < 0.01$. The inflection point parameter (x_0) was calculated from the second derivative of equation 1.

RESULTS

The relationships between respiration rate and root surface area, root mass, and specific surface area were determined for three sugarbeet varieties. Roots were harvested from two field locations that exhibited large variability in root size. Respiration was measured 35 d after harvest to allow any wounds incurred during harvest to heal.

For each variety, roots with low mass had significantly higher respiration rates (Fig. 1). When averaged across the three varieties, respiration rate decreased 48% as root mass increased from 0.3 to 1.0 kg. The relationship between root mass and respiration rate was best characterized with a sigmoidal curve; R^2 values were 0.55, 0.40, and 0.47 for KW 2249, VDH 46177, and Beta 4818, respectively. The nonlinear regression parameter estimates for these sigmoidal relationships
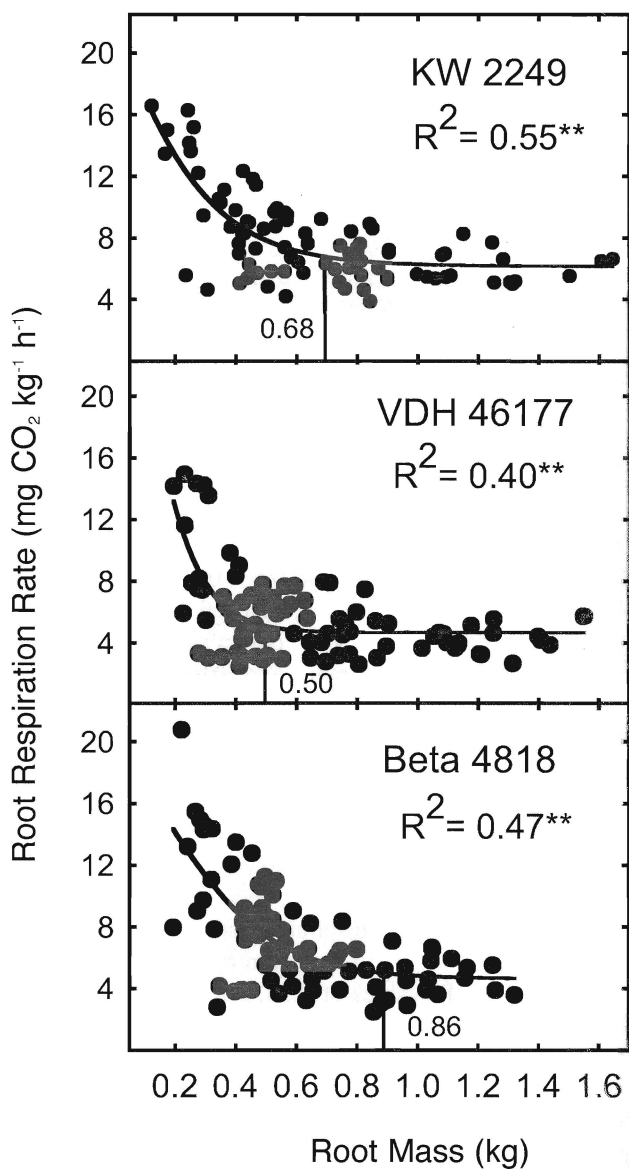
Fig. 1. The relationship between root mass and postharvest root respiration rate for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). The vertical drop line for each variety represents the inflection point of the sigmoidal curve.
** Significant at $P < 0.01$

Table 1. Nonlinear regression coefficients describing the relationship of root mass (Mass), surface area (SFC), and specific surface area (SP SFC) with root respiration rate where respiration rate = y_o + a/(1+e$^{-[(x-x_o)/b]}$).

Cultivar	x	a	b	x_0	y_0	R^2
KW 2249	Mass	45.7	-0.2	-0.1	6.2	0.55**
	SFC	26.4	-122	48.3	6.1	0.38**
	SP SFC	9.5	106	879	5.7	0.57**
VDH 46177	Mass	44.6	-0.1	0.1	4.7	0.40**
	SFC	30.8	-57.8	45.4	4.4	0.29**
	SP SFC	19.1	117	754	3.8	0.34**
Beta 4818	Mass	21.9	-0.2	0.2	4.6	0.47**
	SFC	65.8	-58.3	31.8	4.6	0.39**
	SP SFC	7.4	58.6	487	4.9	0.36**

** significant at $P<0.01$

using the second derivative of the equations describing the curves. Root masses at the inflection points were 0.68, 0.50, and 0.86 kg for KW 2249, VDH 46177, and Beta 4818, respectively (Fig. 1). As mass increased beyond the inflection point, only a small decrease in root respiration rate was observed. Averaged across the three varieties, a 9.5% decrease in respiration was observed from the inflection point to the lower asymptote of the sigmoidal curve, defined hereafter as the baseline respiration value. The baseline respiration value of hand-harvested KW 2249 (6.2 mg CO_2 kg^{-1} h^{-1}) was higher than those of VDH 46177 (4.7 mg CO_2 kg^{-1} h^{-1}) and Beta 4818 (4.6 mg CO_2 kg^{-1} h^{-1}), both of which were from the same location and machine harvested (Fig. 1).

Similar to trends in root mass, decreasing root surface area was also associated with increased respiration rate (Fig. 2). The relationship between root surface area and respiration rate was best described by a sigmoidal curve with R^2 values of 0.38, 0.29, and 0.39 for KW 2249, VDH 46177, and Beta 4818, respectively. Root surface areas at the inflection points of the curves were 377, 235, and 239 cm^2 for KW 2249, VDH 46177, and Beta 4818, respectively (Fig. 2). As surface area increased beyond the inflection point, respiration rate decreased an average of 23% for the three varieties. Hand-harvested KW 2249 roots had a larger range in surface area (122 to 858 cm^2), when compared to machine harvested VDH 46177 (108 to 490 cm^2) and Beta 4818 (143 to 397 cm^2) that had root tips broken during harvest.

While root mass and surface area provided simple measures of root size, the ratio of surface area to mass or specific surface area is a
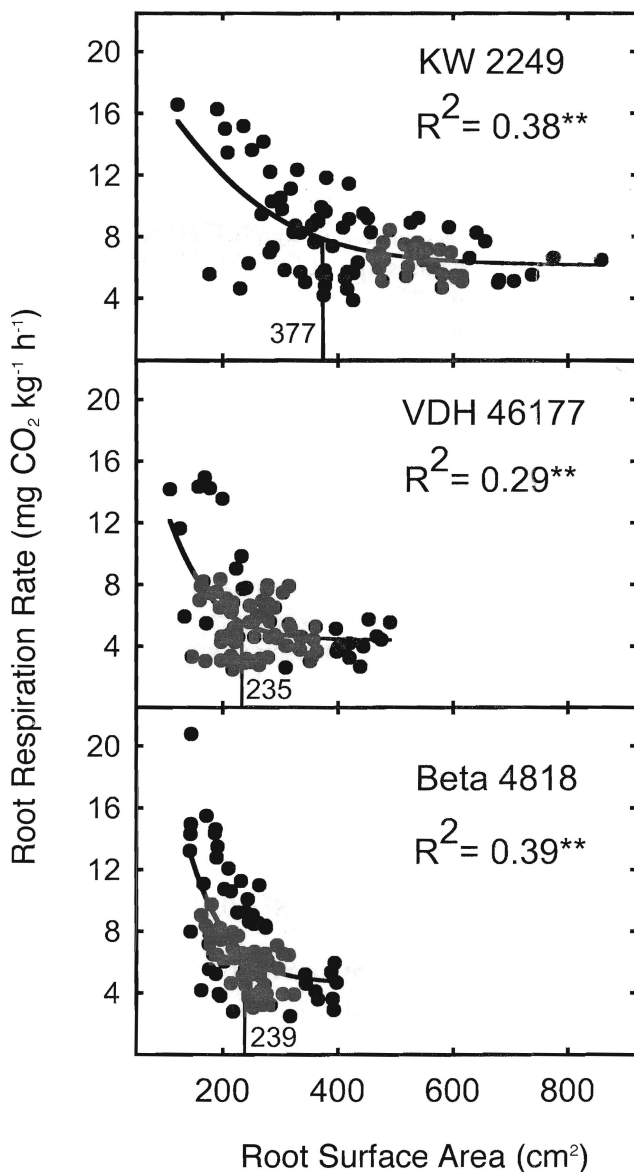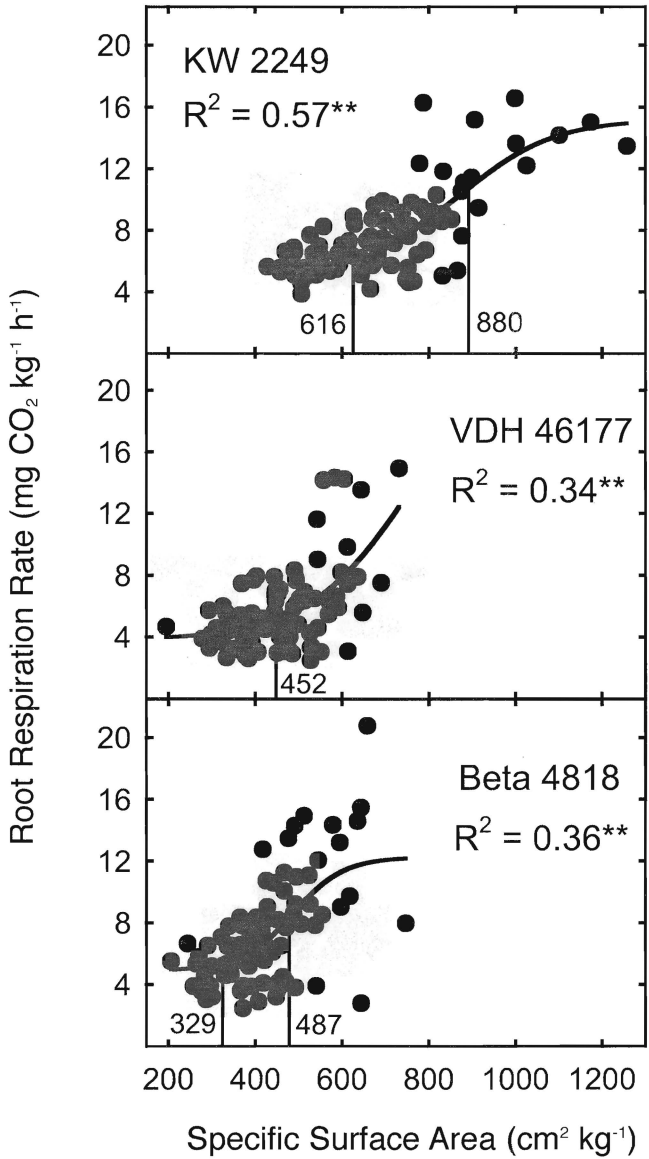
Fig. 2. The relationship between root surface area and sugarbeet postharvest root respiration rate for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). The vertical drop line for each variety represents the inflection point of the sigmoidal curve. ** Significant at $P < 0.01$.

description encompassing both root mass and shape as a single function. Thus, the specific surface area decreases as roots become larger. Assuming similar tissue density in all roots, the specific surface area also decreases as roots become more round, since the ratio of surface area to volume is lowest for a sphere. Although root mass and surface area were negatively associated with respiration rate, the specific surface area was positively associated with respiration rate (Fig. 3). For all varieties, specific surface area was significantly related to respiration rate by a sigmoidal relationship with R^2 values of 0.57, 0.34, and 0.36 for KW 2249, VDH 46177, and Beta 4818, respectively (Fig. 3). For the range of specific surface areas observed in this study, the curves for KW 2249 and Beta 4818 had both lower and upper inflection points, while the curve for VDH 46177 had only a lower inflection. Specific surface areas at the lower inflection points of the curves were 616, 452 and 329 cm^2 kg^{-1} for KW 2249, VDH 46177, and Beta 4818, respectively (Fig. 3). Specific surface areas at the upper inflection points were 880 cm^2 kg^{-1} for KW 2249 and 487 cm^2 kg^{-1} for Beta 4818.
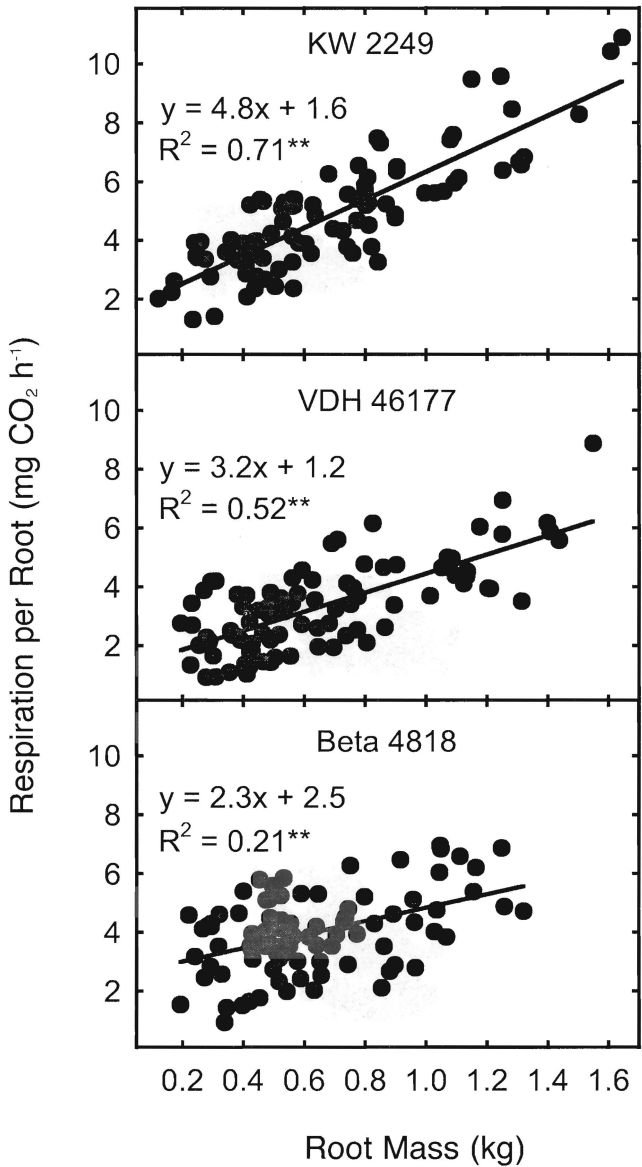
      The relationships between total root respiration and root mass, surface area and specific surface area were also determined for the three sugarbeet varieties (Figs. 4 to 6). Where previous relationships examined a measure of root size against respiration rate expressed as a function of root mass (mg CO_2 kg^{-1} h^{-1}), total root respiration described the respiration rate of the entire root (mg CO_2 h^{-1} $root^{-1}$). Total root respiration was associated with root mass (Fig. 4), surface area (Fig. 5) and specific surface area (Fig. 6) for all three varieties via linear relationships. Total root respiration for KW 2249, VDH 46177, and Beta 4818 was positively associated with root mass (R^2 = 0.71, 0.52, and 0.21; Fig. 4) and surface area (R^2 = 0.72, 0.46 and 0.11; Fig.5) and negatively associated with specific surface area (R^2 = 0.33, 0.29, and 0.15; Fig. 6).

DISCUSSION

The objective of this study was to characterize the relationships between sugarbeet root size and postharvest respiration, and to use these relationships to improve our understanding of root morphological mechanisms controlling respiration. Root mass, surface area, specific surface area, and respiration were measured on 90 individual roots possessing a range of sizes from each of three varieties. Root mass, surface area, and the specific surface area were associated with respiration rate by sigmoidal relationships. There was a critical root size above which size had a limited impact on respiration rate. This critical root size, determined by the inflection point of the sigmoidal curve, was 0.68,
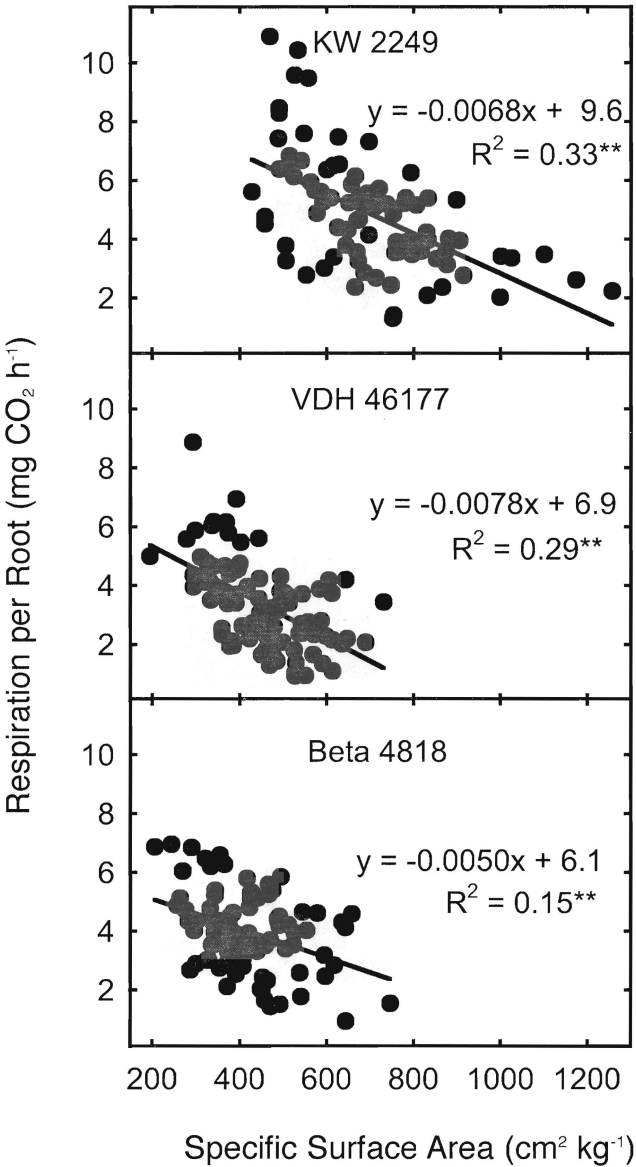
Fig. 3. The relationship of specific surface area and root respiration for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). The specific surface area is calculated as the ratio of beet surface area to mass ($cm^2\ kg^{-1}$). The vertical drop lines for each variety represent inflection points of the sigmoidal curve. ** Significant at $P < 0.01$.

Fig. 4. Relationship between root mass and total root respiration for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). Total root respiration is respiration per root. ** Significant at $P < 0.01$.
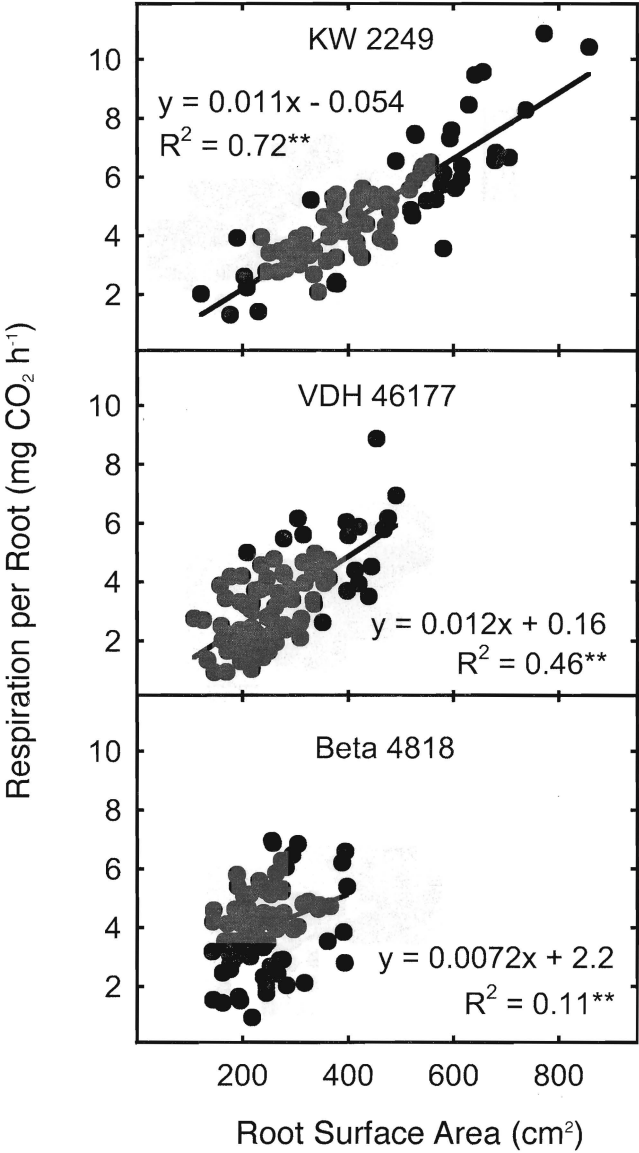
Fig. 5. Relationship between root surface area and total root respiration for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). Total root respiration is respiration per root. ** Significant at $P < 0.01$.

Fig. 6. Relationship between root specific surface area and total root respiration for three sugarbeet varieties: KW 2249, VDH 46177, and Beta 4818 (90 individuals per variety). Total root respiration is respiration per root; specific surface area is calculated as the ratio of beet surface area to mass (cm^2 kg^{-1}). ** Significant at $P < 0.01$.

relationships. There was a critical root size above which size had a limited impact on respiration rate. This critical root size, determined by the inflection point of the sigmoidal curve, was 0.68, 0.50, and 0.86 kg for KW 2249, VDH 46177, and Beta 4818, respectively. Below this critical size, root respiration rate increased substantially as root mass or surface area decreased. Root mass, surface area and specific surface area were also associated with total root respiration by linear relationships. Total respiration was positively associated with root mass and surface area, and negatively associated with specific surface area.

The observed relationship between increased respiration rate and decreasing root size is consistent with most earlier evaluations of sugarbeet respiration rate during storage (Stout, 1954; Wyse and Dilley, 1973; Koster et al., 1980), but contrasts with the results of Wyse et al. (1978). In studies conducted by Wyse and Dilley (1973) and Koster et al. (1980) using roots of two sizes, respiration rate was observed to be greater in smaller roots than in larger roots. Similarly, Stout (1954), using roots of four size classes, found respiration rates to be greater in smaller roots, with the effect of root size on respiration rate greater at smaller root masses (0.3 and 0.5 kg) than at larger root masses (1.1 and 2.2 kg) and best described by a curvilinear relationship. In contrast, Wyse et al. (1978) reported no correlation between respiration rate and root mass among 97 breeding lines. In their study, however, roots were sufficiently large (0.8 to 1.9 kg) that respiration rates would be expected to be minimally affected by differences in root size, and differences in respiration rate related to size may have been masked by differences related to genotype.

It has been theorized in earlier studies that observed relationships between respiration rate and root size are evidence that sugarbeet root respiration is limited by the rate of oxygen and/or carbon dioxide diffusion through the bulky taproot, and that specific surface area best describes the relationship between respiration rate and root size (Stout, 1954; Koster et al., 1980). Root mass, however, generally provided a better description of the relationships of root size with respiration rate for KW 2249, VDH 46177, and Beta 4818 (R^2 = 0.55, 0.40, and 0.47; Fig. 1) than specific surface area (R^2 = 0.57, 0.34, and 0.36; Fig. 3). Similarly, total root respiration was more closely associated with root mass for KW 2249, VDH 46177 and Beta 4818 (R^2 = 0.71, 0.52, and 0.21; Fig. 4) than specific surface area (R^2 = 0.33, 0.29, and 0.15; Fig. 6). Root mass was also more closely associated with respiration rate and total respiration than surface area despite evidence that tissue near the root surface respires more rapidly than internal root tissues (Klotz et al., 2003). For KW 2249, VDH 46177 and Beta 4818, coefficients of deter-

mination for the relationships between surface area and respiration rate were 0.38, 0.29, and 0.39 (Fig. 2); for the relationships between surface area and total respiration, R^2 values were 0.72, 0.46, and 0.11 (Fig. 5).

Although sigmoidal curves described all relationships between root size and respiration rate, and root size was linearly associated with total respiration for all varieties, the relationships of respiration rate and total root respiration with root mass, surface area and specific surface area differed for each variety. Consequently, equations describing these relationships and the inflection points and baseline respiration rates derived from these equations were different for the three varieties. These differences in relationships, inflection points and baseline respiration values among varieties may be attributed to genotype, harvest method, or location effects. Roots of KW 2249 were hand harvested from a field in Fargo, ND; roots of VDH 46177 and Beta 4818 were machine harvested from a field in Foxhome, MN. Previous research has identified significant differences in respiration due to genetic variation (Theurer et al., 1978; Wyse et al., 1978), harvest methods that differ in the extent of injury they deliver to roots (Wyse and Peterson, 1979; Steensen and Augustinussen, 2003), and location effects due to environmental or cultural differences (Wyse et al., 1978). Irregardless of the cause for the different relationships observed between varieties in this study, it is evident that no single equation accurately describes the relationship between root size and respiration during storage.

The results of this study demonstrate that respiration rate and total root respiration are related to root size. The impact of root size on storage respiration rate, however, is likely to be minimal for healthy roots produced using current cultural guidelines. Such roots are of sufficient size that size-related differences in respiration rate are expected to be minor. Field diseases, adverse environmental conditions during production, and growth at high plant populations, however, often result in the production of small roots. For these roots, elevated storage respiration rates are predicted.

ACKNOWLEDGEMENTS

that may be suitable.

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