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Air-filled Porosity, Gas Relative Diffusivity, and Tortuosity: Indices of *Prunus* ×*cistena* sp. Growth in Peat Substrates

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Abstract. **A 2-year experiment with *Prunus* ×*cistena* sp. was conducted in pots using seven substrates composed of various proportions of primarily peat, compost and bark. Peat substrates significantly affected root and shoot dry weight. Water desorption characteristics and saturated hydraulic conductivity were measured in situ to estimate the pore tortuosity factor and the relative gas diffusion coefficient. The pH, electrical conductivity, C/N ratio, total and hydrolyzable N, as well as NO_3^--N and NH_4^+-N in solution were also measured. Estimates of the physical properties suggest that a lack of aeration limited plant growth. Plant growth was significantly correlated with both the gas relative diffusivity and the pore tortuosity factor. Among the chemical factors, pH and soil nitrate level were also correlated with plant growth. No significant correlation was found between plant growth and air-filled porosity or any other measured chemical properties. This study indicates that an index of gas-exchange dynamics could be a useful complementary diagnostic tool to guide substrate manufacturing.**

Nursery plants are generally grown in artificial mixes, composed of two or more components. Many studies have focused on the performance of different media and the growth of nursery plants. There is a general consensus that plant growth is optimized when pH is between 5.0 and 6.5 (except for acid-loving plants) and salt levels are lower than 2 $mmhos \cdot cm^{-1}$ (Goh and Haynes, 1977).

A low C/N ratio (25–30) is also desirable since substrates with high C/N ratios tend to decompose and lose their structure rapidly. Moreover, they tend to immobilize N (Kostov et al., 1991), which may decrease plant growth. As long as pH, salt levels and the C/N ratio are maintained at acceptable levels, chemical properties rarely limit plant growth since nutrient addition via fertigation can adequately supply plant needs.

The physical quality of a substrate is related essentially to its ability to adequately store and supply air and water to ornamental plants grown in pots. The storage and supply of air and water are controlled by pore size abundance, tortuosity, and continuity. Physical properties are of great concern because when inadequate, they cannot be changed easily. Also, aeration problems are frequently encountered by growers (Hanan et al., 1981). Substrate performance has often been linked to physical properties and this relationship has resulted in numerous investigations into the physical properties of potting soils.

Reliable indices characterizing pore space organization are critical as a guide to substrate manufacturing. Many attempts have been made to correlate plant growth with indices of pore space organization describing air and water storage, such as air-filled porosity (f_a) and water retention. Bilderback (1985), Tilt et al. (1987), and Tomlinson (1985) found that plant growth was significantly correlated with the water retention properties of substrates. In an experiment with *Ficus* sp., the plant grew better when the water potential was kept high (–1 to –10 kPa) rather than low (–10 to –30 kPa (De Boodt and De Waele, 1968). Substrates with the lowest f_a were generally associated with the poorest growth (Ouimet et al., 1990; Puustjärvi, 1969; Tilt et al., 1987; Tomlinson, 1985).

Other studies failed to relate f_a and water retention to plant growth (Brown and Emino, 1981; Karlovich and Fonteno, 1986). Glinski and Lipiec (1990) argued that the gas-exchange rate between the atmosphere and the rhizosphere was a more sensitive parameter than gas storage characteristics for assessing the performance of substrates. Indeed, adequate O_2 and CO_2 exchange rates are required for optimum plant growth. Roots respond to reductions in gas diffusion by retarding growth and immediately stopping the initiation and distribution of new roots (Blackwell and

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Wells, 1983; Logsdon et al., 1987). Research has therefore attempted to define a reliable gas-exchange index for plant growth. Blackwell and Wells (1983) and Hodgson and MacLeod (1989), for example, obtained better relationships with growth using oxygen diffusion rates rather than f_a.

The soil-gas diffusivity has often been used as an index of soil aeration. The soil-gas diffusivity for a given gas in a soil (D_s) is commonly expressed relative to the diffusivity of this same gas in free air (D_o) as the gas relative diffusivity (D_s/D_o). Although potentially useful, values of D_s/D_o are difficult to obtain due to the fragile pore space of artificial mixes. Present estimation techniques require substrate manipulation that may disturb the substrate physical properties to be characterized. Recently, Paquet et al. (1993) and Allaire et al. (1994) have developed in situ methods for characterizing pore space organization (pore size distribution and continuity) without sample disturbance. Such methods could be used to provide reliable estimates of soil-gas diffusivity.

Since aeration is often critical to plant growth and commercial substrates frequently vary in physical quality (Bugbee and Frink, 1983; Fonteno et al., 1981), the objectives of this study were to compare the performance of seven substrates with different physical properties and to relate their performance to some indices characterizing gas and water storage and exchange.

Theory for Developing a Gas Relative Diffusivity

For artificial mixes, Eq. [1] provides an adequate description of the water desorption characteristics for water potentials lower than the point of air entry:

$$\theta_v = A + B^{C(\psi - D)} \qquad [1]$$

where θ_v is the volumetric water content, ψ is the water potential (kPa), and A, B, C, and D are empirical constants.

Eq. [1] can be log-transformed as follows:

$$\ln(\theta_v - A) = C(\psi + D)\ln B \qquad [2]$$

Solving for ψ gives

$$\psi = \frac{\ln(\theta_v - A)}{C\ln B} - D \qquad [3]$$

From Jurin's law of capillary rise, it is known that

$$\psi \approx \frac{3}{2r} \qquad [4]$$

where r is the radius of the pores in cm. Combining Eqs. [3] and [4] results in

$$\frac{\ln(\theta_v - A)}{C\ln B} - D = \frac{3}{2r} \qquad [5]$$

Solving Eq. [5] for r and squaring each side of the equation yields

$$r^2 = \left(\frac{1.5C\ln B}{\ln(\theta_v - A) - CD\ln B}\right)^2 \qquad [6]$$

and r^2 is computable for any volumetric water content using the parameters of the water desorption characteristics for a media.

The saturated hydraulic conductivity (K_s) is often modelled on the pore-size distribution,

$$K_s = \frac{100\rho g}{8\eta\tau}\sum_{i=1}^{n}\left(\Delta\theta_v\right)_i r_i^2 \qquad [7]$$

where K_s is the saturated hydraulic conductivity ($cm \cdot s^{-1}$), η is the water viscosity ($Pa \cdot s^{-1}$), ρ is the water density ($g \cdot cm^{-3}$), τ is the pore tortuosity coefficient, $\Delta\theta_v$ is the volumetric water content for pores having a mean pore radius of r in the pore class i ($m^3 \cdot m^{-3}$), and the factor τ is a weighing coefficient that is used to take (into account) two factors: 1) some pores are dead-end pores that do not participate in transport (Glinski and Stepniewski, 1985), and 2) the real pathway followed by water is longer than the apparent one (Koorevaar et al., 1983). The pore tortuosity coefficient is assumed constant in Eq. [7] and thus the medium is assumed rigid during the measurement, which appears a reasonable assumption, when substrates are submitted to multiple wetting and drying cycles (Bragg and Chambers, 1988).

Since the expression

$$\frac{100\rho g}{8\eta}\sum_{i=1}^{n}\left(\Delta\theta_v\right)_i r_i^2 = K_s\,\tau \qquad [8]$$

Table 1. Volumetric composition ($m^3 \cdot m^{-3}$) of experimental substrates

Substrate	Peat	Bark[z]	Sand[y]	Compost[v]	Sawdust	Mould[x]	Gravel[w]
S1	40	---	20	0	40	---	---
S2	52	33	10	5	---	---	---
S3	60	25	10	5	---	---	---
S4	0	50	20	10	---	20	---
S5	40	30	---	10	---	---	20
S6	30	60	10	---	---	---	---
S7	30	50	15	5	---	---	---

[z] Coniferous composted bark.

[y] The grain size was <2 mm.

[x] The mould is highly organic top soil.

[w] The grain size was between 4–8 mm.

[v] The nature of the compost varies between the substrates.

represents pore flow in straight tubes, it can be seen that the coefficient τ is an empirical coefficient reducing pore flow to fit measured K_s values.

Eq. [7] can be rewritten into an integral form as

$$\tau = \frac{100\rho g}{8\eta K_s}\int_{\theta vl}^{\theta va} f(\theta)d\theta \qquad [9]$$

where

$$f(\theta) = r^2 \qquad [10]$$

and θ_{va} and θ_{vl} are calculated as follows:

$$\theta_{va} = A + B^{C(0.35 - D)} \qquad [11a]$$

and

$$\theta_{vl} = A + B^{C(5.0 - D)} \qquad [11b]$$

The value of 0.35 kPa in the calculation of θ_{va} is the air entry value and the 5.0 kPa value in the θ_{vl} calculation is arbitrarily fixed as the integral lower limit since values exceeding 5.0 kPa have little influence on the results of the integral. Since $f(\theta)$ is obtained from Eq. [6] and K_s is measured, τ can be calculated from Eq. [9]. Some authors use the pore effectiveness for water flow (γ) instead of τ, and $\gamma = 1/\tau$.

D_s/D_o can then be derived from the relationship (King and Smith, 1987)

$$\frac{D_s}{D_o} = \gamma^* f_a^{\mu} \qquad [12]$$

where D_s and D_o are the gas diffusivity in soil and air respectively ($cm^3 \cdot cm^{-1} \cdot s^{-1}$), μ is an empirical parameter approximately equal to one in peat (King and Smith, 1987), γ^* is the pore effectiveness coefficient for gas diffusion, and f_a is the air-filled porosity.

Assuming that the empirical coefficient μ varies little between substrates and assuming that $\gamma \approx \gamma^*$ (assumptions to be discussed later in the results and discussion section), D_s/D_o of individual substrates can therefore be calculated directly as follows:

$$\frac{D_s}{D_o} = \gamma(f_a) \qquad [13]$$

where g and f_a are derived from measurements of water flow and desorption characteristics of the substrate. The D_s/D_o coefficient can therefore be used as an index of the gas-exchange dynamics in substrates by measuring K_s and water retention in pots.

Materials and Methods

Plant growth. An experiment comparing seven substrates was set up at Laval Univ. in 1991. Each experimental unit was composed of five pots. The pots were arranged in a randomized complete block design replicated three times. As described by Allaire et al. (1994), 5-liter containers were filled by hand with substrates (S1–S7) and planted with rooted stem cuttings of *Prunus ×cistena* sp. The substrates were fabricated using easily available components varying in particle size and shape and chemical properties, a common practice in the artificial mix industry, and this variation led to differences in substrate aeration and other properties (Tables 1 and 2). The compost type varies among substrates. S2 and S3 contained composted sewage sludge, S4 contained composted paper sludge, S5 had composted cattle manure, and S7 contained composted tree leaves.

Substrates were top-dressed with a slow release fertilizer (Nutricote, Chiso-Asahi Fertilizer Company, Tokyo) at a rate of 25 g/pot at the beginning of each year. Nutricote is a resin coated fertilizer containing $14N–14P_2O_5–14K_2O$ of type 180 where the

Table 2. Initial physical and chemical properties of experimental substrates.

Substrate	f_a [z] ($m^3 \cdot m^{-3}$)	EAW ($m^3 \cdot m^{-3}$)	RW ($m^3 \cdot m^{-3}$)	TP ($m^3 \cdot m^{-3}$)	K_s ($cm^3 \cdot s^{-1}$)	τ ($m \cdot m^{-1}$)	D_s/D_o ($m^2 \cdot s^{-1} \cdot m^{-2} \cdot s^{-1}$)	C/N	pH
S1	0.31	0.09	0.36	0.76	0.500	30.0	0.010	28.5	5.8
S2	0.20	0.15	0.43	0.79	0.094	29.0	0.006	24.9	6.4
S3	0.28	0.13	0.40	0.82	0.046	30.6	0.009	46.4	5.4
S4	0.42	0.07	6.37	0.86	0.079	23.5	0.018	30.1	5.8
S5	0.29	0.09	0.40	0.78	0.087	16.7	0.017	33.3	5.8
S6	0.30	0.11	0.41	0.82	0.064	25.7	0.012	48.2	5.8
S7	0.30	0.09	0.42	0.81	0.028	40.1	0.008	27.3	5.8

	Particle size distribution ($kg \cdot kg^{-1}$)					
Substrate	<1 (mm)	1–4 (mm)	4–8 (mm)	8–16 (mm)	16–25 (mm)	>25 (mm)
S1	0.79	0.16	0.04	0.01	0.00	0.00
S2	0.83	0.10	0.04	0.02	0.01	0.00
S3	0.78	0.11	0.07	0.03	0.01	0.00
S4	0.76	0.14	0.06	0.03	0.00	0.01
S5	0.66	0.13	0.17	0.04	0.00	0.00
S6	0.81	0.09	0.06	0.04	0.00	0.00
S7	0.83	0.12	0.04	0.01	0.00	0.00

[z] f_a = Air-filled porosity, EAW = easily available water, RW = residual water, TP = total porosity, K_s = saturated hydraulic conductivity, τ = pore tortuosity factor, and D_s/D_o = gas relative diffusivity.

Table 3. Physical and chemical properties of seven ornamental substrates after 2 years of production.

		Substrate								
		S1	S2	S3	S4	S5	S6	S7	LSD(0.05)	CV
					Physical properties[y]					
f_a[z]	$m^3{\cdot}m^{-3}$	0.14	0.06	0.12	0.14	0.16	0.12	0.10	0.04	24
EAW	$m^3{\cdot}m^{-3}$	0.21	0.18	0.22	0.14	0.18	0.22	0.21	0.05	14
RW	$m^3{\cdot}m^{-3}$	0.37	0.42	0.39	0.40	0.40	0.36	0.41	0.05	7
TP	$m^3{\cdot}m^{-3}$	0.74	0.78	0.77	0.66	0.74	0.73	0.76	0.04	4
K_s	$cm{\cdot}s^{-1}$	0.05	0.06	0.097	0.105	0.108	0.10	0.069	0.05	44
τ	$m{\cdot}s^{-1}$	23.0	12.0	9.0	9.0	11.0	9.0	13.0	12.0	51
D_s/D_o	$m^2{\cdot}s^{-1}{\cdot}m^{-2}{\cdot}s^{-1}$	0.006	0.007	0.013	0.017	0.014	0.014	0.008	0.006	40
					Chemical properties[y]					
EC	$dS{\cdot}m^{-1}$	3.3	4.5	2.5	7.6	3.9	9.2	1.7	3.6	68
C/N		22.0	22.0	24.0	17.0	24.0	21.0	27.0	5.0	25
pH		4.30	4.53	4.95	5.35	4.69	4.46	4.32	0.03	76
Total N	$g{\cdot}kg^{-1}$	0.102	0.173	0.144	0.155	0.158	0.176	0.118	0.034	16
Hyd. N	$g{\cdot}kg^{-1}$	0.084	0.112	0.096	0.149	0.105	0.122	0.084	0.046	19
NH_4^+-N	ppm	45	64	45	155	69	201	54	140	90
NO_3^--N	ppm	670	600	390	270	720	290	210	NS	63

[z] f_a = Air-filled porosity, EAW = easily available water, RW = residual water, TP = total porosity, K_s = saturated hydraulic conductivity, τ = pore tortuosity factor, D_s/D_o = gas relative diffusivity, and EC = electrical conductivity, Hyd. N = hydrolyzable N.

[y] The means were calculated from three observations.

type indicates the normal release time in days. A 1 liter liquid fertilizer application at a concentration of 300 $mg{\cdot}liter^{1}$ of N from a solution of 20–20–20 (which corresponded to 0.20 $g{\cdot}g^{-1}$ of N, 0.132 $g{\cdot}g^{-1}$ of P, 0.166 $g{\cdot}g^{-1}$ of K, 0.001 $g{\cdot}g^{-1}$ of Fe, 0.0005 $g{\cdot}g^{-1}$ of Mn, 0,0005 $g{\cdot}g^{-1}$ of Zn, 0.0005 $g{\cdot}g^{-1}$ of Cu, 0.0002 $g{\cdot}g^{-1}$ of B and 0.000005 $g{\cdot}g^{-1}$ of Mo) was carried out weekly. Water was supplied at a rate of 1 liter per irrigation per pot using a drip irrigation system when the potential reached –5.0 kPa, as measured by vertically inserted tensiometers. This fertilization and irrigation scheme was found to be adequate for all substrates since this scheme showed maximum or near maximum plant growth parameters (root, shoot, and plant height) for all substrates in a companion study. Further details regarding the effect of irrigation and fertilization practices on substrate performance can be found in Anonymous (1993). Shoot dry weight (SDW) and root dry weight (RDW) were measured in one pot per experimental unit after two years of growth.

Physical properties. All physical properties of the substrates were measured in situ i.e. directly in the pot immediately after planting (Table 2) or during plant growth (Table 3). Measurements were carried out on only 1 pot per experimental unit per treatment. Water desorption curves were determined using vertically inserted tensiometers and time domain reflectometry (TDR) probes (Paquet et al., 1993). Additional measurements were taken in two pots from each of four treatments selected randomly (S1, S2, S5, and S7) at the end of the growth period. Dielectric constant (Ka) readings of TDR were converted into volumetric water contents using Paquet's equation for pooled substrates (Table 5 in Paquet et al., 1993).

Water desorption curves were estimated using Eq. [2] for y < –0.35 kPa. For y ≥ –0.35 kPa, θ_v was considered equal to total porosity since the air entry value was estimated at –0.35 kPa. The air entry value was determined in an independent laboratory experiment carried out directly in pots with the coarser and the finer substrates sitting on a tension table (Paquet et al., 1993). This value was assumed to apply to all substrates.

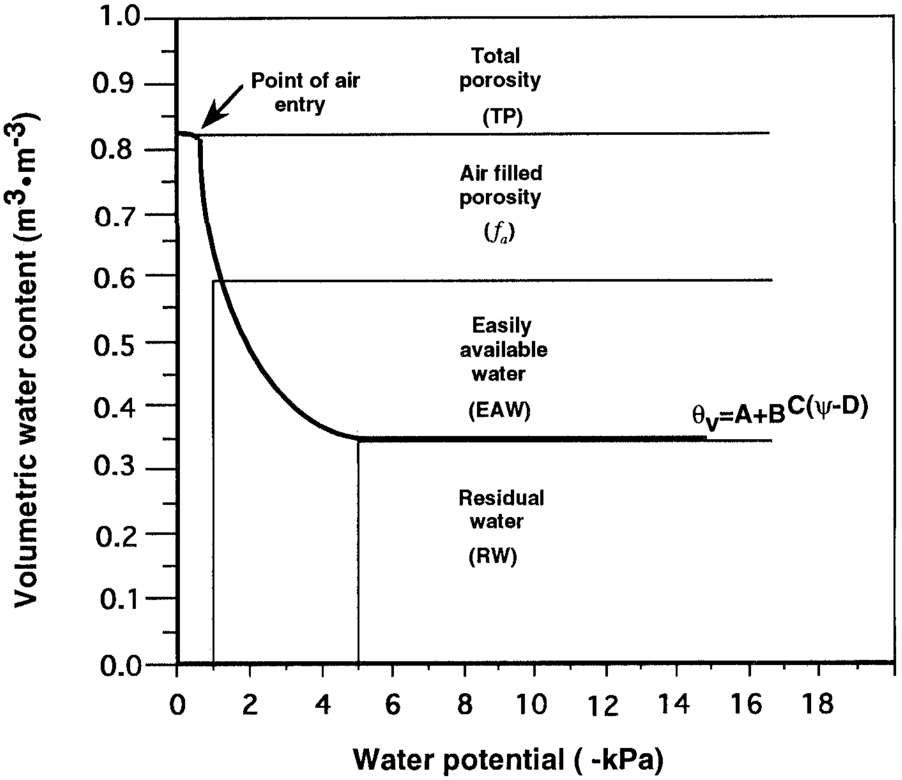

Fig. 1. Example of an idealized water retention curve.

Total porosity (TP), air-filled porosity (f_a), easily available water (EAW), and residual water (RW) were derived from the water retention curves (Fig. 1). For the f_a calculation, the lower water potential was set at –0.8 kPa, a value corresponding to the potential measured at half height of the pot after saturating and then draining it for 2 h. For EAW, the lower limit was set at –5.0 kPa according to De Boodt and Verdonck (1972). The following equations were subsequently used to compute the physical properties of the substrates:

$$TP = A + B^{-CD} \qquad [14]$$

$$f_a = TP - \left(A + B^{C(0.8 - D)}\right) \qquad [15]$$

$$EAW = TP - f_a - \left(A + B^{C(5.0 - D)}\right) \qquad [16]$$

$$RW = A + B^{C(5.0 - D))} \approx A \qquad [17]$$

Saturated hydraulic conductivity (K_s) was measured in the pots that were used for the water desorption curves, as described by Allaire et al. (1994). Oxygen diffusion rates were measured with a platinum electrode (Lemon and Erickson, 1952) and calculated with the following equation:

$$ODR = \frac{i{*}10^{-6} M}{nFA} \qquad [18]$$

where i is the electrical current (mA), *M* is the molecular weight of gas (32 g·mol^{-1} for oxygen), *n* is the number of electrons required for the reduction of one molecule of gas (4 for oxygen), *F* is the Faraday constant (96500 C/equiv.), and *A* is the surface area of the electrode (4 cm^2). Particle size distribution was estimated by wet sieving, according to Dinel and Levesque (1976).

Chemical properties. Soil solution was extracted from the saturated media (Warncke, 1986) and analyzed for electrical conductivity. Substrate pH was measured directly in the saturated paste (Page et al., 1982). The initial pH had been adjusted from 5.4 to 6.4 using dolomitic lime. NH_4-N and NO_3-N analysis were performed by steam distillation after reducing nitrates using Devarda's alloy (Bremmer and Mulvaney, 1982). Hydrolyzable N was extracted using 6 M HCl, followed by Devarda's alloy (Bremmer and Mulvaney, 1982). Total N was analyzed by the micro-Kjeldahl method followed by steam distillation (Bremmer and Mulvaney, 1982). Total C was analyzed from the loss on ignition at 550C for 16 h after drying the soil at 105C for 24 h (De Rouin, 1988).

Table 4. Comparison of shoot dry weight (SDW) and root dry weight (RDW) of *Prunus* ×*cistena* sp. in seven substrates after 2 years of production.

	Parameter	
Substrate	SDW (g)	RDW (g)
S1	51.0	17.3
S2	85.3	20.6
S3	105.3	26.9
S4	78.5	21.9
S5	117.6	28.7
S6	93.1	25.3
S7	91.8	27.1
LSD(0.05)	12.5	5.5

*Statistical analysis***.** Statistical analyses and regression equations were conducted using SAS/STAT Release package version 6.03 (SAS Institute, Cary, N.C.). A randomized complete block design with data from 1 pot per experimental unit was used, for a total of 21 observations (7 substrates × 3 replications). For the correlations and multiple regressions, all additional data (two additional pots per experimental unit for S1, S2, S5, and S7) were used, for a total of 45 observations (21 + 4 substrates × 2 pots × 3 replications). One observation was deleted because it was found to be an outlier using the maximum normal residual test (MNR) of Snedecor and Cochrane (1989). Least square methods were used to fit Eq. [1] to the measured data using Mathcad software package version 4.0 (Mathsoft, Cambridge, Mass.). Calculations of Eq. [9] were performed using the same software.

Results and Discussion

Significant differences in plant growth were found between substrates after 2 years of production (Table 4). The highest shoot dry weights were obtained with S5 and S3 while the lowest values were obtained with S1 and S4. Similarly, S1, S2, and S4 had the lowest root dry weights while S5, S7, and S3 had the highest ones. After two years, substrates showed significant differences in all of their chemical and physical characteristics (Table 3), as was expected since they were manufactured from components differing in physical and chemical characteristics. Variability appeared to be particularly high for K_s, D_s/D_o, τ, electrical conductivity, and pH, as well as for NH_4^+-N and NO_3^--N concentrations.

Chemical and physical variables were correlated to plant growth parameters using simple linear regressions (Table 5). Among the physical properties, only τ and D_s/D_o were significantly correlated to plant growth. Substrate pH and soil nitrates were the two chemical properties significantly correlated to shoot dry weight. Using stepwise multiple regressions to look at possible simulta-

Table 5. Correlation coefficient between shoot dry weight (SDW) and root dry weight (RDW) and chemical and physical properties (n = 44)

	SDW	RDW
	Physical properties	
f_a^{z}	0.03^{NS}	0.27^{NS}
EAW	0.08^{NS}	0.09^{NS}
RW	0.10^{NS}	–0.16^{NS}
τ	–0.49**	–0.32*
D_s/D_o	0.42**	0.38*
	Chemical properties	
EC	–0.08^{NS}	0.01^{NS}
pH	0.42**	0.20^{NS}
Total N	0.29^{NS}	–0.01^{NS}
Hyd. N	0.03^{NS}	–0.10^{NS}
NH_4^+-N	–0.25^{NS}	–0.07^{NS}
NO_3-N	–0.37*	–0.22^{NS}

^{z} f_a = Air-filled porosity, EAW = easily available water, RW = residual water, τ = pore tortuosity factor, D_s/D_o = gas relative diffusivity, and EC = electrical conductivity, Hyd. N = hydrolyzable N.

^{NS,*,**}Nonsignificant or significant at $P = 0.05$ and 0.01, respectively.

Table 6. Summary of stepwise multiple regressions relating plant growth parameters to physical and chemical properties (n = 44).

Variable	Intercept	Estimated parameter	Partial R^2	Estimated parameter	Partial R^2	Total R^2
RDW^z	13.59	1701 $D_s/D_o{}^{*}$	0.12	–50570 $D_s/D_o{}^{2*}$	0.08	0.20
SDW	116	–1.82 τ^{**}	0.25	–0.0029 $NH_4{}^{+NS}$	0.05	0.30

^{z}SDW = shoot dry weight, RDW = root dry weight.

^{NS,*,**}Nonsignificant or significant at P = 0.05, 0.01, respectively.

neous relationships between chemical and physical parameters and plant growth, only D_s/D_o, τ, and $NH_4{}^+$-N were found to be significant explicative variables for SDR and RDW (Table 6).

The high coefficients of variation given in Table 4 suggest that the methods used to measure tortuosity and K_s were highly variable, which may have increased the error term and thus decreased the correlation. Also, a correlation may be poor due to the fact that this is the flux of oxygen into or the flux of CO_2 out of the root zone that is going to influence plant growth. In this study, the flux of oxygen itself was not measured, but only the resistance to the flux itself, within the substrate (D_s/D_o). Since the flux of the oxygen or the CO_2 will depend only partially on the soil resistance to gas diffusion, then, the correlation with plant growth is also expected to be partial.

The results regarding the superiority of D_s/D_o over f_a support the conclusion of Paul and Lee (1976) who found that a dynamic process such as the oxygen diffusion rate would correlate more closely with plant growth than f_a. Brown and Emino (1981) found significant differences in the growth of six ornamental species among substrates, differences that could not be explained by the chemical or physical properties they studied (f_a and EAW alone).

The quadratic least square fit of D_s/D_o suggests that an increase in D_s/D_o up to a maximum value near 0.015 resulted in an increase in root growth (Fig. 2). The removal of an extreme value (D_s/D_o = 0.27) still resulted in a quadratic relationship between D_s/D_o and RDW. Increasing pore tortuosity may have decreased shoot dry weight (Fig. 3). Longer pathways for gas diffusion to or from the rhizosphere may have affected shoot growth. Low gas diffusivity may have led to an oxygen shortage affecting metabolic processes in whole plants (Glinski and Stepniewski, 1985).

The following facts support the view that oxygen might have influenced *Prunus* ×*cistena* sp. growth in this experiment: 1) Air storage and exchange were more likely to be limiting than water storage and exchange when water was supplied regularly; 2) ODR measurements were in the range of 4 to 12 × 10^{-8} g O_2/cm^2 per min, a level reported to limit the growth of *Chrysanthemum* sp. (Paul and Lee, 1976), and the tortuosity factor τ was negatively correlated to ODR measurements (r = –0.45, P < 0.10), indicating that τ apparently limited the oxygen diffusion toward the root, as expected from the theory; and 3) measured values (0.06–0.16 $cm^3 \cdot cm^{-3}$) were within the range in which plants are likely to be affected by substrate aeration status (<0.10–0.15 $cm^3 \cdot cm^{-3}$) according to Bunt (1988) and Verdonck and Gabriëls (1991). The lowest but significant contribution of $NH_4{}^+$-N in the multiple regression and $NO_3{}^-$-N in the simple correlation suggests that chemical properties may have affected plant growth, but to a lesser extent than the physical properties. The correlation of $NH_4{}^+$-N and $NO_3{}^-$-N with plant growth may also indicate less removal of nutrients by smaller plants.

The practical implications of these findings are important since f_a is the common aeration status index used to guide substrate manufacturing. This study indicates that an index of gas-exchange dynamics could provide a useful complementary diagnostic tool in addition to air-filled porosity to guide substrate manufacturing. This is supported by the fact that air-filled porosity was not correlated to plant growth, even if it covered a range of values (0.07 to 0.20 $cm^3 \cdot cm^{-3}$) that is likely to affect plant growth (Bunt, 1988). With the method used herein, the index is based on direct measurements in pots, therefore avoiding substrate disturbance. In situ measurements of the physical conditions affecting plant growth can thus be obtained repeatedly throughout the rooting media. This provides an important advantage over the point estimate provided by ODR measurements when investigating substrate gas-exchange properties.

Further work should be conducted to establish causal relationships between plant growth and τ or D_s/D_o. Also, D_s/D_o estimation should be improved. It was based on the assumptions that $\mu = 1$, $\gamma \approx \gamma^*$, and the point of air entry is equal to –0.35 kPa, all of which deserve further investigation since differences between air entry values will obviously affect gas diffusivity estimation from Eq. [13] and then the performance of D_s/D_o as a predictor of plant growth parameters may be changed.

So far, the approach proposed here for estimating D_s/D_o from K_s and water desorption characteristics have produced g estimates (0.02 to 0.20) consistent with γ^* values (0.08–0.165) reported for peat substrates by King and Smith (1987). This consistency indicates a promising avenue for D_s/D_o estimation from K_s and water desorption characteristic measurements.

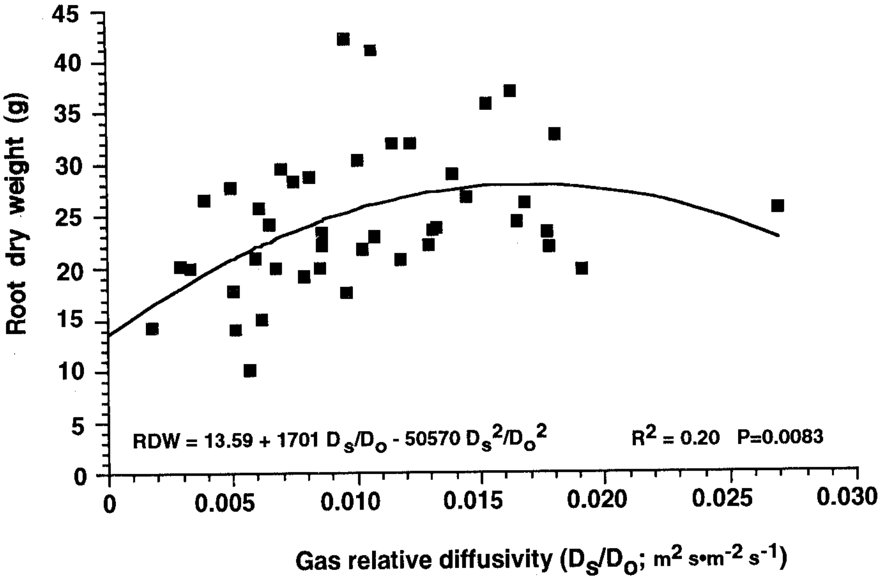

Fig. 2. Relationship between gas relative diffusivity (D_s/D_o) and root dry weight (RDW).

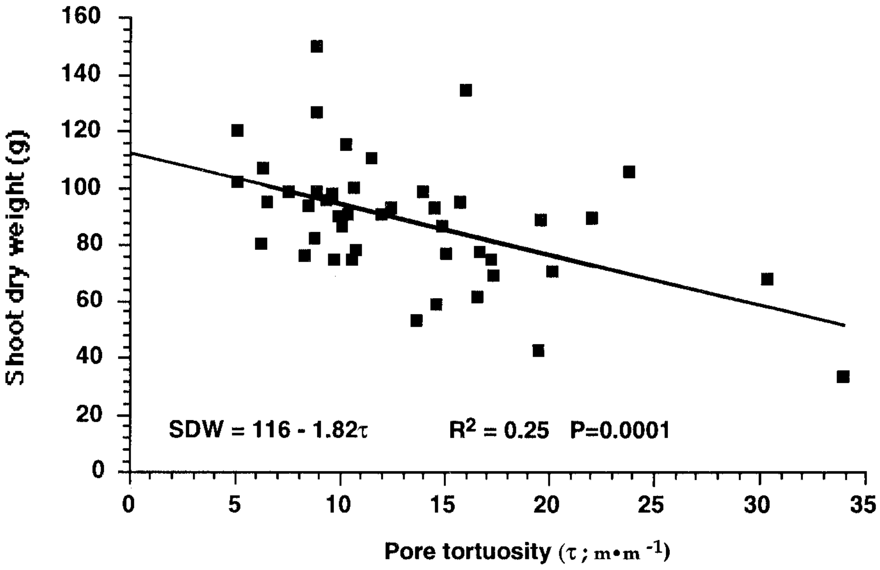

Fig. 3. Relationship between pore tortuosity (τ) and shoot dry weight (SDW).

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