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

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Additional index words. gas diffusivity, pore tortuosity, peat mixes, compost, nursery production

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 NO3\textsuperscript{–}, NH4\textsuperscript{+} and pH 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·cm\textsuperscript{–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. Bilderkamp (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). Gliński 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\textsubscript{2} and CO\textsubscript{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...
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 $f_g$.

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:

$$\theta_v = A + B C(\psi - D)$$

[1]

where $\theta_v$ is the volumetric water content, $\psi$ is the water potential (kPa), and $A$, $B$, $C$, and $D$ are empirical constants. Eq. [1] can be log-transformed as follows:

$$\ln(\theta_v - A) = C(\psi + D)\ln B$$

[2]

Solving for $\psi$ gives

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

[3]

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

$$\psi \approx \frac{3}{2r}$$

[4]

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

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

[5]

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

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

[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,

$$K_s = \frac{100\rho g}{8\eta \sum_{i=1}^{n} (\Delta \theta_i^v) r_i^2}$$

[7]

where $K_s$ is the saturated hydraulic conductivity (cm·s$^{-1}$), $\eta$ is the water viscosity (Pa·s$^{-1}$), $\rho$ is the water density (g·cm$^{-3}$), $\tau$ is the pore tortuosity coefficient, $\Delta \theta_i^v$ is the volumetric water content for pores having a mean pore radius of $r$ in the pore class $i$ (m$^3$·m$^{-3}$), and the factor $\tau$ 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

$$K_s = \frac{100\rho g}{8\eta \sum_{i=1}^{n} (\Delta \theta_i^v) r_i^2} = K_s \tau$$

[8]

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

| Substrate | Peat | Bark* | Sand* | Compost* | Sawdust | Mould* | Gravel* |
|-----------|------|-------|-------|-----------|---------|--------|---------|
| 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    | 15    | 5         | ---     | ---    | ---     |
| S7        | 30   | 50    | 15    | 5         | ---     | ---    | ---     |

*Coniferous composted bark.
†The grain size was <2 mm.
‡The mould is highly organic top soil.
§The grain size was between 4–8 mm.
¶The nature of the compost varies between the substrates.
represents pore flow in straight tubes, it can be seen that the coefficient $\tau$ is an empirical coefficient reducing pore flow to fit measured $K_s$ values. 

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

$$
\tau = \frac{100 \rho g}{8 \eta K_s} \int_{\theta v a}^{\theta v l} f(\theta) d\theta
$$

where

$$f(\theta) = r^2$$

and $\theta_{va}$ and $\theta_{vl}$ are calculated as follows:

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

and

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

The value of 0.35 kPa in the calculation of $\theta_{va}$ is the air entry value and the 5.0 kPa value in the $\theta_{vl}$ 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, $\tau$ can be calculated from Eq. [9]. Some authors use the pore effectiveness for water flow ($\gamma$) instead of $\tau$, and $\gamma = 1/\tau$.

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

$$
\frac{D_s}{D_o} = \gamma f_a
$$

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–14P₂O₅–14K₂O of type 180 where the

| Substrate | $f_a$ (m³·m⁻³) | EAW (m³·m⁻³) | RW (m³·m⁻³) | TP (m³·m⁻³) | $K_s$ (cm·s⁻¹) | $\tau$ (m·m⁻¹) | $D_s/D_o$ (m²·s⁻¹·m⁻²) | 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|

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

| 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    |

$\gamma$ and $f_a$ are air-filled porosity, EAW = easily available water, RW = residual water, TP = total porosity, $K_s$ = saturated hydraulic conductivity, $\tau = \text{pore tortuosity factor}$, and $D_s/D_o = \text{gas relative diffusivity}$. 

$D_s$ and $D_o$ are the gas diffusivity in soil and air respectively (cm³·cm⁻¹·s⁻¹), $\mu$ is an empirical parameter approximately equal to one in peat (King and Smith, 1987), $\gamma’$ is the pore effectiveness coefficient for gas diffusion, and $f_a$ is the air-filled porosity.
type indicates the normal release time in days. A 1 liter liquid fertilizer application at a concentration of 300 mg·liter⁻¹ of N from a solution of 20–20–20 (which corresponded to 0.20 g·g⁻¹ of N, 0.132 g·g⁻¹ of P, 0.166 g·g⁻¹ of K, 0.001 g·g⁻¹ of Fe, 0.0005 g·g⁻¹ of Mn, 0.0005 g·g⁻¹ of Zn, 0.0002 g·g⁻¹ of Cu, 0.0002 g·g⁻¹ of B and 0.000005 g·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, θₜ 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.

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 | | | | | | | | | |
| fₐ | m³·m⁻³ | 0.14 | 0.06 | 0.12 | 0.14 | 0.16 | 0.12 | 0.10 | 0.04 | 24 |
| EAW | m³·m⁻³ | 0.21 | 0.18 | 0.22 | 0.14 | 0.18 | 0.22 | 0.21 | 0.05 | 14 |
| RW | m³·m⁻³ | 0.37 | 0.42 | 0.39 | 0.40 | 0.40 | 0.36 | 0.41 | 0.05 | 7 |
| TP | m³·m⁻³ | 0.74 | 0.78 | 0.77 | 0.66 | 0.74 | 0.73 | 0.76 | 0.04 | 4 |
| Kₛ | cm·s⁻¹ | 0.05 | 0.06 | 0.097 | 0.105 | 0.108 | 0.10 | 0.069 | 0.05 | 44 |
| τ | m⁻¹ | 23.0 | 12.0 | 9.0 | 9.0 | 11.0 | 9.0 | 13.0 | 12.0 | 51 |
| D/Dₛ | m⁻³·s⁻¹ | 0.006 | 0.007 | 0.013 | 0.017 | 0.014 | 0.014 | 0.008 | 0.006 | 40 |
| Chemical properties | | | | | | | | | |
| EC | dS·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·kg⁻¹ | 0.102 | 0.173 | 0.144 | 0.155 | 0.158 | 0.176 | 0.118 | 0.034 | 16 |
| Hyd. N | g·kg⁻¹ | 0.084 | 0.112 | 0.096 | 0.149 | 0.105 | 0.122 | 0.084 | 0.046 | 19 |
| NH₄⁺-N | ppm | 45 | 64 | 45 | 155 | 69 | 201 | 54 | 140 | 90 |
| NO₃⁻-N | ppm | 670 | 600 | 390 | 270 | 720 | 290 | 210 | NS | 63 |

¹ fₐ = Air-filled porosity, EAW = easily available water, RW = residual water, TP = total porosity, Kₛ = saturated hydraulic conductivity, τ = pore tortuosity factor, D/Dₛ = gas relative diffusivity, and EC = electrical conductivity, Hyd. N = hydrolyzable N.

² The means were calculated from three observations.
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:

$$TP = A + B - CD$$  \[14\]

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

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

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

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:

$$ODR = \frac{i \times 10^{-6} M}{n FA}$$  \[18\]

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/eqiv.), 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, according to 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 550°C for 16 h after drying the soil at 105°C for 24 h (De Rouin, 1988).

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

| Parameter              | SDW | RDW |
|------------------------|-----|-----|
| Substrate              |     |     |
| 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|

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 $K_s$, $D_s/Do$, $\tau$, 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 $\tau$ and $D_s/Do$ were significantly correlated to plant growth. Substrate pH and soil nitrites were the two chemical properties significantly correlated to shoot dry weight. Using stepwise multiple regressions to look at possible simulta-
neous relationships between chemical and physical parameters and plant growth, only D/Do, τ, and NH₄⁺-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 Kₛ 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 CO₂ 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/Do) where the flux of the oxygen or the CO₂ will depend 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/Do over fa 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 fa. 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 (fa and EAW alone).

The quadratic least square fit of D/Do suggests that an increase in D/Do up to a maximum value near 0.015 resulted in an increase in root growth (Fig. 2). The removal of an extreme value (Ds/Do = 0.27) still resulted in a quadratic relationship between D/Do and SDR or 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 (Gliński and Stepniewski, 1985).

The following facts support the view that oxygen might have influenced Prunus ×sikkimensis 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 O₂/cm² 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 cm³·cm⁻¹) were within the range in which plants are likely to be affected by substrate aeration status (<0.10–0.15 cm³·cm⁻¹) according to Bunt (1988) and Verdonck and Gabriëls (1991). The lowest but significant contribution of NH₄⁺-N in the multiple regression and NO₃⁻-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 NH₄⁺-N and NO₃⁻-N with plant growth may also indicate less removal of nutrients by smaller plants.

The practical implications of these findings are important since fa 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 cm³·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/Do. Also, D/Do estimation should be improved. It was based on the assumptions that μ = 1, γ = γ*, 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/Do as a predictor of plant growth parameters may be changed.

So far, the approach proposed here for estimating D/Do from Kₛ 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/Do estimation from Kₛ and water desorption characteristic measurements.

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

| Variable   | Intercept   | Estimated parameter | Partial R²  | Estimated parameter | Partial R²  | Total R² |
|------------|-------------|---------------------|-------------|---------------------|-------------|----------|
| SDW        | 13.59       | 1701 D₃/Do⁻¹        | 0.12        | −50570 D₃/Do⁻²     | 0.08        | 0.20     |
| SDW        | 116         | −1.82 τ*²           | 0.25        | −0.0029 NH₄⁺*      | 0.05        | 0.30     |

'SDW = shoot dry weight, RDW = root dry weight.

* Significant at $P = 0.05, 0.01$, respectively.
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