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Full Length Research Paper

Pore space organization and plant response in peat substrates: II. *Dendrathemum morifolium* Ramat

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Plant growth response to substrate physical properties may be influenced not only by storage (water and air contents), but also by the exchange properties of the substrate. We studied the effect of variably sized components on substrate storage and exchange properties and related plant growth to these properties. Four substrates were composed of 40% coniferous bark (CB), 50% peat and 10% gravel. Peat and gravel particle size remained constant, but coniferous bark particle size was varied (1 - 2, 2 - 4, 4 - 8 and 8 - 16 mm). *Dendrathemum morifolium* Ramat plants were transplanted in aluminum cylinders measuring 9.6 cm in diameter and 10.1 cm in height. The substrates were subjected to three (-0, -1.6 and 3.2 kPa) water potentials. Pore tortuosity factor (τ) increased linearly (P=0.0001) with increasing bark particle size while the relative gas diffusion coefficient (D_s/D_o) decreased (P=0.0068). Air-filled porosity (f_a) remained unaffected by bark particle size. *D. morifolium* Ramat growth parameters were correlated to substrate exchange properties with correlation coefficients ranging from 0.24 to 0.91. This study confirms the existence of a causal relationship between plant growth and bark size that is likely due to a modification of the substrate exchange properties. The results also suggest that the effect of the substrate exchange properties on plant response is prevalent even over a short period of growth.

Key words: Gas diffusivity, pore tortuosity, air-filled porosity, peat substrates, peat-lite mixes, *Dendrathemum morifolium.*

INTRODUCTION

In a previous study, we showed that substrate particle size had a very significant effect on the pore tortuosity factor (τ) and relative gas diffusivity coefficient (D_s/D_o) and that these two parameters, in turn, had a very significant effect the growth of two perennial woody landscape species (*Spiraea japonica* 'Little Princess' and *Prunus x cistena*) in peat substrates (Nkongolo and Caron, 2006). Our results had practical implications for the growth of nursery plants but were obtained over relatively long-term (2 years) trials. Indeed, the results indicated a 50% decrease in plant growth with decreasing diffusivity even if no changes in air-filled porosity were observed. However, because of the pronounced difference in the growth patterns of these species and the fact that substrate physical properties change rapidly, the study needed to be extended to include more species of economical importance but with shorter growth periods, like potted greenhouse species. Consequently, this experiment focused on the effect of bark size on *D. morifolium* Ramat, a potted species with a short-term production cycle.

The response of *Dendrathemum* sp. to substrate storage properties, especially air-filled porosity, has also been extensively investigated. Fonteno and Nelson (1990) showed that *Dendrathemum* grown in rockwool amended media with high air-filled porosity had reduced plant height and width in comparison with media of lower air-filled porosity. Media with the lowest aeration produc-

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Table 1. Composition of experimental substrates.

Substrate	Peat	Bark^z		Gravel^y
	(%)	(%)	Particle size	(%)
S1	50	40	1-2 mm	10
S2	50	40	2-4 mm	10
S3	50	40	4-8 mm	10
S4	50	40	8-16 mm	10

^{z}Coniferous wood bark.
^{y}The grain size was between 4-8 mm.

ed the highest quality rating, fresh weight and shoot. Bowman et al., (1994) found that Dendrathemum (*Dendranthema x grandiflora* Ramat Kitamura) plant height, fresh weight, dry weight and number of open flowers were significantly reduced in rubber-amended media compared to sawdust controls; the former media had higher air-filled porosities and bulk densities. Paul and Lee (1976) used air-filled porosity and oxygen diffusion rate to evaluate the aeration of their media. They investigated the relationship between these two aeration parameters and plant growth and obtained quadratic correlations between *D. morifolium* top growth and both air-filled porosity and the oxygen diffusion rate. Air-filled porosity of media ranged from 0 to 20%. The authors concluded that the best plant growth was obtained with an air-filled porosity of 10 -15%.

Other authors have focused on the relationship between *D. morifolium* growth and substrate water storage characteristics. No differences in final height, top fresh weight, top dry weight, or flower number were observed in *D. morifolium* Ramat. 'Spice' grown in 16.5 cm azalea pots when the substrates were allowed to dry to soil water potentials of -5, -10, -20 or -30 kPa between waterings (Karlovich and Fonteno, 1986). Röber and Hafez (1981) studied the influence of different substrates and water regimes on the growth of *Dendrathemum-Indicum-Hybrids (D. x hortum* L.H. Bailey) and found that shoot height decreased with decreasing moisture in the substrates (increasing aeration). High water contents in the substrates (low aeration) resulted in greater flower and shoot weights. The authors emphasized that the decrease in yield with falling substrate moisture contents was more pronounced in a peat substrate than with peat-clay mixture, although the highest yield was obtained in a peat substrate. Lieth and Burger (1989) reported that a soil water potential of -7.5 or-15 kPa caused significant reductions in the fresh and dry weights of leaves, stems and inflorescences, and in the total leaf area of *D. morifolium* Ramat cv. Polaris plants. They concluded that the -1.5 kPa and -3.5 kPa treatments minimized water use while maintaining high crop productivity.

Based on the above studies, as well as many others (Warren and Fonteno*,* 1993; Tyler et al., 1993), it appears that the assessment of the physical conditions in growing media used for Dendrathemum as well as other horticultural plants has been restricted to storage properties: total porosity, container capacity, air space, and available or unavailable water. However, adequate aeration is necessarily dependent on an adequate air supply from the atmosphere to the rhizosphere and on an elimination of gases from the rhizosphere to the atmosphere. Such gaseous exchanges are controlled by pore space, air-filled porosity, gas diffusion and the gradient of concentration between the atmosphere and the rhizosphere. Therefore, to best correlate plant growth to the physical conditions in the root zone, it is important to assess the variations not only in the storage properties (water and air contents), but also in the exchange (pore tortuosity and gas diffusivity) properties of the substrates. The objective of this study was to evaluate the effect of variable sized components on short-term changes in substrate physical properties and plant growth. A second objective was to investigate possible indices affected by component size that could be used to guide the manufacturing of substrate used for *D. morifolium* plants.

MATERIALS AND METHODS

This experiment was conducted in the growth chambers of the Horticultural Research Centre at Laval University, Quebec, Canada. Four substrates (S1, S2, S3, S4) were prepared by mixing coniferous bark (40% v/v) with sphagnum peat moss (50%) [H2-H3 on the von Post scale (von Post and Granlund, 1926)] and gravel 10% (Table 1). Peat and gravel size remained constant, but coniferous bark particle size varied (1 - 2, 2 - 4, 4 - 8 and 8 - 16 mm) such that each of the four substrates contained a specific particle size, but the same volume of coniferous bark (Table 1). The substrates were chemically amended with 4.8 kgm^{-3} of CaMg(CO3)$_2$ and with a slow release fertilizer (Nutricote, Chiso-Asahi Fertilizer Company, Tokyo) at a rate of 7.5 g/L. Nutricote is a resin coated fertilizer containing N-P_2O_5-K_2O (14-14-14). Aluminum cylinders (radius 4.8 cm, height 10.1 cm) were filled with the four substrates; the bottoms of the cylinder were covered with 1.5 mm aluminum mesh. A total of 36 (4 substrates x 3 water potentials x 3 replications) cylinders containing the substrates were placed into plastic containers covered with a plastic paper on the top. The cylinders were wetted from the bottom with distilled water and allowed to saturate for 72 h. Nine tensions tables were prepared in advance inside the growth chamber (Topp

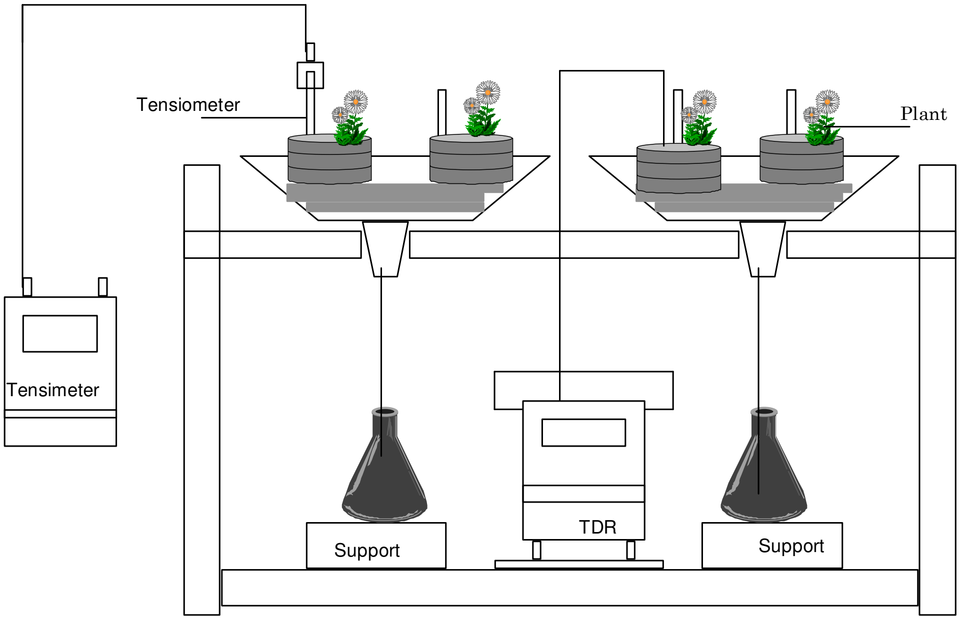

Figure 1. Experimental design.

and Zebchuk, 1979). *Dendrathemum* cuttings were potted (one per cylinder) and provided with a solution of N-P_2O_5-K_2O (20-20-20) at a rate of 200 g/100 L. This fertilization treatment was applied every week throughout the 4 months of the experiment. Four cylinders containing the plants (one per substrate) were put onto each of the tension tables. Three water potentials (0, -1.6, and -3.2 kPa) were maintained. The tension tables were replicated 3 times generating a split- plot design with water potentials as the main plots and substrates as the subplots. A temperature of 21°/18°C (day/night), 80% relative humidity and a 16 h photoperiod were maintained in the growth chamber throughout the experiment. At the end of the experiment, data on plant height were collected, the plant shoots were removed and the substrates were subjected to saturated hydraulic conductivity measurements. Later, the roots were washed, oven-dried and weighed. As the study was conducted on tension tables, data for the water desorption curve were taken throughout the study with tensiometers inserted into each growing medium (Figure 1).

Theoretical background

Nkongolo (1996), Allaire et al. (1996a and b) have suggested a fast method to obtain rough estimates of gas exchanges indices in peat substrates. However, the calculation in Nkongolo (1996), Equation [12] requires multiple measurements for establishing the ψ-θ relationship. However, for peat substrates, the early phase (from saturation to -1 kPa approximately) of water desorption is approximated by a linear equation of the form

$$\theta = a.\psi + b \qquad [1]$$

Where *a* is the slope, b is the intercept and ψ is the soil water potential and can be transformed into an equivalent mean pore radius using Jurin's law (Musy and Soutter, 1991).

$$\psi = \frac{0.03}{2r} \qquad [2]$$

then Equation. [2] can be rewritten as

$$2r = \frac{0.03(a)}{\theta - b} \qquad [3]$$

Isolating r (radius) and squaring both sides yields

$$r^2 = \frac{0.000225a^2}{\theta^2 - 2\theta b + b^2} \qquad [4]$$

substituting Equation [4]. Into Equatuon [3]. gives

$$\tau = \frac{10\rho g}{8\eta Ks} \int_{\theta\,\mathrm{inf}}^{\theta\,\mathrm{sup}} \frac{0.000225a^2}{\theta^2 - 2\theta b + b^2} d\theta \qquad [5]$$

Changing variables in Equation [5] with

$$\theta - b = u \qquad [6]$$

$$du = d\theta \qquad [7]$$

and by substitution

$$\tau = \frac{10\rho g}{8\eta Ks} \int_{U_{\inf}+b}^{U_{\sup}+b} \frac{0.000225a^2}{U^2} du \qquad [8]$$

For which the solution is $\frac{-1}{\theta - b} + cte$ (Spiegel, 1981) and then

$$\tau = \frac{10\rho g}{8\eta Ks} * 0.000225a^2 \left(\frac{-1}{\theta - b} \Big|_{\theta_{\inf}}^{\theta_{\sup}} \right) \qquad [9]$$

However, we know that:

$$\theta_{\sup} = a\ \psi_{\sup} \qquad [10]$$

$$\theta_{\inf} = a\ \psi_{\inf} \qquad [11]$$

Therefore

$$\tau = \frac{10\rho g}{8\eta Ks} * 0.000225a^2 \left[\frac{-1}{a\psi_{\sup}} + \frac{1}{a\psi_{\inf}} \right] \qquad [12]$$

$$\tau = \frac{10\rho g}{8\eta Ks} * 0.000225a \left[\frac{\psi_{\sup} - \psi_{\inf}}{\psi_{\sup} * \psi_{\inf}} \right] \qquad [13]$$

Therefore, to estimate τ (and subsquently D_s/D_o) from Equation [13] we have to determine 4 unknowns: *a*, $\theta_{\sup}$, θ_c. and K_s. K_s is directly obtained from water flow (Allaire et al., 1994). The value of *a* is the slope of the linear regression line between ψ and θ (early phase of the water desorption curve) is obtained from two points: θ at the point of air entry (θ_a,ψ_a) and θ and ψ after saturation and drainage (θ_c, ψ_c). Since we know that after saturation and drainage, substrates in cylinders will equilibrate at a potential (in cm) close on average to half height of the substrate in the cylinder, then ψ_c need not to be measured, but can be approximated by half height of the substrate in the cylinder. Also, we can consider that $\theta_a \approx \theta_{\sup}$. Since θ_s and θ_c can be easily measured by time domain reflectometry, and ψ_c estimated, the only unknown left is ψ_a which can be estimated from data in the litterature to be around -0.35 kPa (Allaire et al., 1996 a and b) or from limited measurements for a same substrate samples. Consequently, calculation of *a* yields.

$$a = \frac{\theta_c - \theta_{\sup}}{\psi_c - \psi_a} = \frac{\theta_c - \theta_{\sup}}{\left(\text{half of the height of substrate in pot (kPa)} - \psi_a\right)}$$

[14]

Now, $\psi_{\inf}$ has to be calculated from the relation [11] since a and b are known and $\theta_{\inf}$ is about 0.35 cm^3 cm^{-3} in peat substrates. Therefore, Equation [14] can be rewritten in terms of easily measurable properties K_s, θ_s, and θ_c while $\psi_{\inf}$ is estimated from a and b and ψ_a is approximated with an average value obtained from independent measurement of ψ-θ in early desorption. This yield:

$$\tau = \frac{10\rho g}{8\eta Ks} * 0.000225 * \frac{\theta_c - \theta_{\sup}}{\left(\text{half of the height of substrate in pot (kPa)} - \psi_a\right)} \left[\frac{\psi_{\sup} - \psi_{\inf}}{(\psi_{\sup} * \psi_{\inf}} \right]$$

[15]

and therefore a method to estimate τ from two points measurements can be used. The time needed for such method is considerably shorter since all parameters can be obtained within 2 h. The validation of the method has been published elsewhere (Caron and Nkongolo, 2004).

Volumetric water content at saturation (θ_s)

After saturation of substrate, time domain reflectometry (TDR) probes (13.5 cm long) were inserted at an angle of 25° from the vertical (in order to have complete insertion of the probes) at half height of the substrate to measure its dielectric constant (k_a) according to the procedure of Topp et al. (1980). For peat substrates, the measured k_a was converted into volumetric water content at saturation, (total porosity) as follows (Paquet et al., 1993):

$$\theta = -0.0055+0.0425\ k_a-0.000975\ k^2_a+0.00000907\ k^3_a \qquad [16]$$

for k_a between 5 and 58.

Volumetric water content at container capacity (θ_c)

This was measured after saturation and drainage for 2 h.

Air-filled porosity (f_a)

Air-filled porosity was calculated from the difference between volumetric water content (estimated by TDR) at saturation (θ_s) and that after saturation and drainage (θ_c).

$$f_a = \theta_s - \theta_c \qquad [17]$$

Where f_a = air-filled porosity (cm^3 cm^{-3})

Saturated hydraulic conductivity (K_s)

Saturated hydraulic conductivity was measured according to Allaire et al. (1994).

Measurement of the air-entry value (ψ_a)

The air-entry value was estimated 'from a limited number of substrate samples' since such a procedure has been shown to provide an adequate characterization of τ (Nkongolo, 1996).

Chemical properties

The chemical composition of the experimental substrates was determined at the beginning as well as at the end of the experiment.

Table 2. Initial air and water characteristics ($cm^3\ cm^{-3}$) of experimental substrates (measured at -0.51 kPa).

Substrate	ƒa	CC	TP	AW	EAW	RW
S1 (1-2 mm)	0.18	0.74	0.56	0.26	0.19	0.30
S2 (2-4 mm)	0.19	0.75	0.56	0.24	0.17	0.31
S3 (4-8 mm)	0.18	0.75	0.57	0.26	0.20	0.31
S4 (8-16 mm)	0.20	0.76	0.56	0.27	0.20	0.30
CV	9.16	3.96	6.20	10.50	20.00	7.10
SD	0.03	0.03	0.03	0.03	0.04	0.02

TP = total porosity, CC = container capacity, ƒa = air-filled porosity, AW = available water, EAW = easily available water, RW = residual water.

Table 3. Effect of water potential and wood bark particle size on the chemical conditions of substrates planted with *Chrysanthemum morifolium* after 4 months of production.

Water potential (P)	**pH**	**Salinity (mmho)**
P1 (0.0 kPa)	7.85	1.87
P2 (-1.6 kPa)	6.68	2.06
P3 (-3.2 kPa)	6.65	1.87
Bark[1] particle size (S)		
S1 (1-2 mm)	7.07	1.89
S2 (2-4 mm)	7.13	1.88
S3 (4-8 mm)	6.91	1.96
S4 (8-16 mm)	7.12	1.99

Analysis of variance.

Sources of Variation		**pH**		**Salinity**	
	dl	**F**	**Prob.**	**F**	**Prob.**
Block	2	0.55	0.5848	5.19	0.0166
Water potential (P)	2	91.54	0.0001	1.36	0.2819
P Linear		69.72	0.0001	0.000	0.9947
P Quadratic		25.76	0.0071	4.49	0.1015
Error (a)		0.117		0.834	
Bark particle size (S)	3	1.48	0.2540	0.31	0.8176
Interaction P x S	6	1.13	0.3822	2.24	0.0867
Error (b)	24	0.061		0.138	

[1] Coniferous wood bark

At the beginning, after drying, the substrate samples were ground in a Wiley mill to pass through a 40 mesh (0.425 mm) screen. The concentration of PO_4-P, SO_4-S, Mg, Ca, and K were determined using the Mehlich III method (Mehlich, 1984). The extractant was composed of 0.2 M CH_3COOH, 0.25 M NH_4NO_3, 0.015 M NH_4F, 0.013 M HNO_3, and 0.001 M ethylene diamine tetraacetic acid (EDTA). The concentrations of NO_4-N and NH_4-N were determined using the 2.0 M KCL method. At the end of the experiment, soil solution was extracted from the saturated media (Warnckle, 1986) and analyzed for electrical conductivity (Table 2). Substrate pH (Table 2) was measured directly in the saturated paste (Page et al., 1982). All the substrate analyses were conducted in the chemical analysis laboratory of the Horticultural Research Centre at Laval University, Ste-Foy, Quebec, Canada.

Statistical analysis

Statistical and regression analyses were conducted using the SAS/STAT Release package, Version 6.03 (SAS Institute, Cary, N.C.). A split-plot arrangement was used with water potential (0, -1.6 and -3.2 kPa) levels as the main plots and coniferous bark particle sizes (1 - 2, 2 - 4, 4 - 8, and 8 - 16 mm) as the subplots. The plots were replicated three times for a total of 36 observations (4 bark particle si-

Table 4. Effect of water potential and wood bark particle size on the physical conditions of substrates planted with *Dendrathemum morifolium* Ramat after 4 months of production.

Water potential (P)	**K_s (cm s^{-1})**	**f_a (cm^3 cm^{-3})**	**τ (cm cm^{-1})**	**D_s/D_o (cm^2 s^{-1} cm^{-2} s)**
P1 (0.0 kPa)	0.095	0.01	26.05	0.0004
P2 (-1.6 kPa)	0.097	0.22	26.81	0.0082
P3 (-3.2 kPa)	0.083	0.25	26.80	0.0093
Bark particle size (S)				
S1 (1-2 mm)	0.083	0.15	22.36	0.0067
S2 (2-4 mm)	0.092	0.16	23.78	0.0067
S3 (4-8 mm)	0.096	0.15	27.99	0.0054
S4 (8-16 mm)	0.096	0.16	33.41	0.0048

Analysis of variance.

		K_s		**f_a**		**τ**		**D_s/D_o**	
Sources of Var.		**F**	**Prob**	**F**	**Prob**	**F**	**Prob**	**F**	**Prob**
Block	2	0.98	0.39	2.28	0.126	0.90	0.409	3.4	0.053
Water potential (P)	2	0.45	0.64	1.26	0.000	1.30	0.275	144	0.000
P Linear (PL)		1.2	0.32	247	0.000	2.7	0.113	278	0.000
P Quadratic (PQ)		0.68	0.45	5.60	0.027	0.90	0.384	10	0.004
Error (a)	4	0.0029		83.92		0.335		0.0005	
Bark part. size (S)	3	0.20	0.89	0.02	0.997	33	0.000	5.3	0.006
S Linear (SL)		0.36	0.55	0.49	0.978	97	0.000	15	0.001
S Quadratic (SQ)		0.22	0.64	0.00	0.983	1.70	0.207	0.44	0.514
Interaction									
P x S	6	0.32	0.92	0.32	0.918	1.20	0.370	2.2	0.087
P L x S L		0.04	0.85	0.00	0.991	0.64	0.431	5.8	0.025
Error (b)	24	0.0061		684.4		6.79		21.10^{-6}	

f_a = Air-filled porosity, K_s = saturated hydraulic conductivity, τ = pore tortuosity factor, D_s/D_o = gas relative diffusivity coefficient.

zes x 3 water potentials x 3 replications). Computations were performed using Mathcad software package, Version 4.0 (Mathsoft, Cambridge, Mass.).

RESULTS AND DISCUSSION

Chemical properties in the substrates: The chemical properties of the susbstrates after four months of experiment were analyzed and are presented in Table 3. Data for chemical properties at the beginning of the experiment are not presented. Neither water potential nor increasing coniferous bark particle size affected any of the parameters studied, with the exception of pH which decreased linearly with increasing water potential.

Physical conditions in the substrates. For the initial physical properties, data are omitted for clarity since the trends observed at the end of the growing period were the same as those observed at the beginning. Physical properties measured after 4 months of growth revealed that increasing coniferous bark particle size from 1 - 2 to 8 -16 mm in the media (Table 4) did not affect air-filled porosity and saturated hydraulic conductivity, but significantly affected pore tortuosity and relative gas diffusivity. Pore tortuosity increased linearly while relative gas diffusivity decreased with increasing coniferous bark particle size in the substrates. These results are in agreement with those of Bunt (1988), Handreck (1983) and Bowman et al. (1994) who did not observe a change in the air-filled porosity of their media when using mineral and organic particles of larger sizes. The air-filled porosity and gas relative diffusivity increased linearly with increasing water potential whereas τ and K_s remained unaffected by water potential.

Plant growth parameters: *D. morifolium* plant height (PHT), shoot dry weight (SDW) and root dry weight (RDW) were all very significantly affected by both water potential and coniferous bark particle size (Table 5). The response of both PHT and SDW to increasing coniferous bark in media depended on the water potential applied as shown

Table 5. Effect of water potential and wood bark particle size on plant height (PHT), root dry weight (RDW) and shoot dry weight (SDW) of *Dendrathemum morifolium* Ramat after 4 months of production.

Water potential (P)	**PHT (cm)**	**SDW (mg)**	**RDW (mg)**
P1 (0.0 kPa)	23.29	40.41	20.49
P2 (-1.6 kPa)	31.31	50.60	30.05
P3 (-3.2 kPa)	24.08	40.07	30.32
Bark particle size (S)			
S1 (1-2 mm)	28.83	50.61	30.80
S2 (2-4 mm)	26.00	40.72	30.15
S3 (4-8 mm)	25.44	40.36	20.61
S4 (8-16 mm)	24.63	40.08	20.25

Analysis of variance

		PHT		**SDW**		**RDW**	
Sources of Variation	**df**	**F**	**Prob**	**F**	**Prob**	**F**	**Prob**
Block	2	1.18	0.329	1.56	0.236	.59	0.565
Water potential (P)	2	38.07	0.000	9.92	0.001	15.72	0.000
P Linear		0.15	0.714	4.13	0.111	46.23	0.002
P Quadratic		19.04	0.012	89.19	0.000	1.87	0.243
Error (a)	4	24.40		0.166		0.0907	
Bark particle size (S)	3	4.88	0.011	5.09	0.010	29.71	0.000
S Linear		9.61	0.006	11.11	0.003	74.73	0.000
S Quadratic		3.11	0.095	3.17	0.092	13.32	0.001
Interaction							
P x S	6	3.01	0.032	4.53	0.005	0.54	0.771
P Linear x S Linear		3.97	0.061	15.85	0.000	0.89	0.359
P Quad x S Linear		6.90	0.017	4.64	0.045	0.05	0.823
Error (b)	24	6.151		0.782		0.139	

Table 6. Correlation coefficient between *Dendrathemum morifolium* Ramat plant height (PHT), shoot dry weight (SDW) and root dry weight (RDW) and some physical properties of substrates after 4 months of production.

Physical parameters	**PHT**	**SDW**	**RDW**
(f_a)	0.103^{NS}	0.123^{NS}	0.089^{NS}
(τ)	0.347***	0.908****	0.863****
(D_s/D_o)	0.277**	0.634****	0.644****

f_a = Air-filled porosity, τ = pore tortuosity factor, D_s/D_o = gas relative diffusivity coefficient.
^{NS}nonsignificant or significant at P=0.01, 0.001 and 0.0001, respectively.

by a PxS significant interaction (Table 5). PHT (0.0124) and SDW (p=0.0001) increased quadratically with increasing aeration (decreasing water potential) whereas RDW (P=0.0024) increased linearly. *D. morifolium* PHT (P=0.0062), SDW (P=0.0037) and RDW (P=0.0001) all decreeased linearly as coniferous bark particle size increased in the media (Table 5). These results are in agreement with those reported by Bowman et al. (1994) who observed *Dendrathemum* plant height, number of open flowers per pot and dry weight to decrease as either coarse or fine ground automobile tires particles increased in the media. The decrease in the plant growth parameters as coniferous bark particle size increased in the media can be explained by the increase in pore tortuosity and the reduction in gas diffusivity (Table 4) since increase in tortuosity has been related to a decreased oxygen diffusion rate (Allaire et al., 1996).

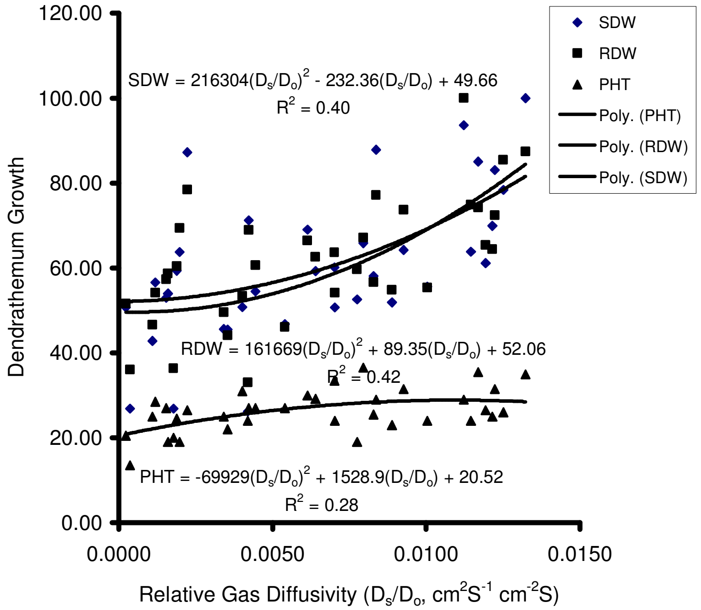

Figure 2. Relationship between plant shoot dry weight (SDW), shoot dry weight (RDW) and plant height (PHT) expressed as a % of maximum growth and Relative Gas Diffusion Coefficient (Ds/Do).

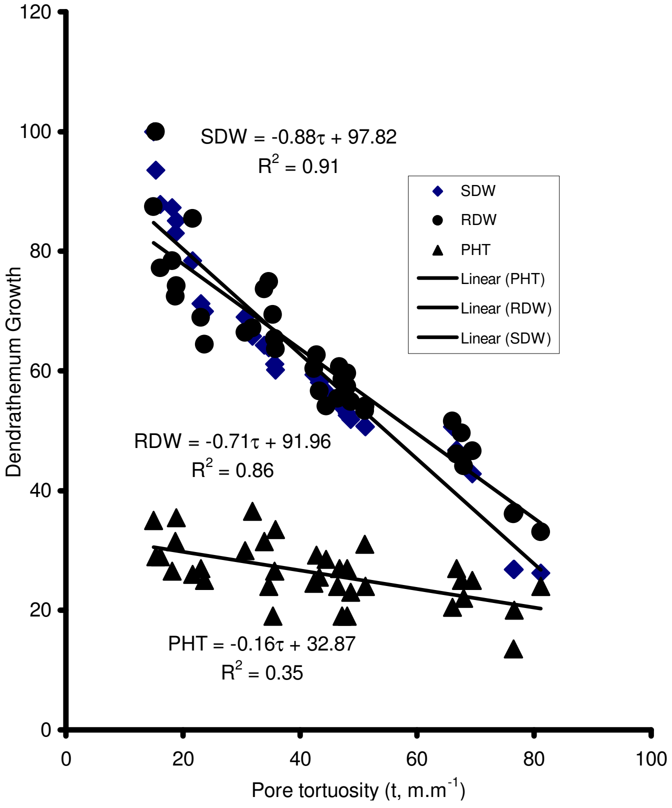

Figure 3. Relationship between plant shoot dry weight (SDW), shoot dry weight (RDW) and plant height (PHT) expressed as a % of maximum growth and pore tortuosity.

Correlation between plant growth and some of the physical properties of the media: Can some measurable physical properties be used to guide substrate manufacturing? Neither SDW nor RDW of *D. morifolium* could be correlated to air-filled porosity (Table 6). However, Plant height (PHT) was strongly correlated with τ (P = 0.0001, $R^2 = 0.347$) and D_s/D_o (P = 0.0001, $R^2 = 0.277$). *D. morifolium* SDW was highly correlated with τ (P = 0.0001, $R^2 = 0.908$) and D_s/D_o (P = 0.0001, $R^2 = 0.634$) and finally *D. morifolium* RDW (Figure 2) was highly correlated with τ (P = 0.0001, $R^2 = 0.863$) and D_s/D_o (P = 0.0001, $R^2 = 0.644$). Except for air-filled porosity, the results obtained for this second experiment correspond with those of a previous study (Nkongolo et al., 1995). The lack of correlation between the *Dendrathemum* growth parameters and air-filled porosity is again an indication that not only the storage, but also the gas exchange properties should be taken into account when assessing the physical conditions in media (Figure 3).

Practical Implications

In this study as well as in those of Nkongolo (1996) and Allaire et al. (1996a and b), the substrate gas exchange indices were well correlated to plant growth parameters, but air-filled porosity could not be correlated with plant growth. The practical implication of these findings is important since the effect of bark size on plant growth is confirmed. Gas exchange properties should therefore be measured to obtain an accurate assessment of the physical conditions in substrates whether or not air-filled porosity is adequate.

Conclusion

This study demonstrates that increasing bark particle size from 1 - 2 mm to 8 - 16 mm significantly affects substrate gas relative diffusivity and pore tortuosity without affecting air-filled porosity. The study also shows that varying component size influences plant response, most likely by its effect on gas exchange dynamics, and that some indices of gas exchange dynamics are closely correlated to plant growth. The study confirms the results previously obtained by Nkongolo and Caron (2006) with *Prunus* and *Spiraea*, and supports the existence of a causal relationship between plant growth and substrate gas exchange properties. This study shows that the effect of substrate gas exchange properties on plant response is prevalent even over a short growth period. It is therefore recommended that D_s/D_o and τ be measured in addition to air-filled porosity when evaluating the suitability of media for plant growth.

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