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BEHAVIOR OF *IMPATIENS WALLERANA* HOOK. F IN ALTERNATIVE POT SUBSTRATES: MECHANISMS INVOLVED AND RESEARCH PERSPECTIVES

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□ *The approach to select new growing media, has been focused on selecting materials only from the physical point of view. The objective of this study was to describe the physiological mechanisms involved in* I. wallerana *growth when cropped on a broad range of growing media created from alternative components. Results showed a close relationship between I.* wallerana *growth and fine particle size at the beginning of the experiments. Shoot fresh weight was determined mainly by the root system size. There were small differences in the relative growth rate (RGR) between the control substrate and the thirty alternative substrates tested. The lower RGR values resulted from a decrease in the net assimilation rate and the leaf area ratio. The mechanism involved would be associated with a change in photosynthate partitioning, which favored root growth. A close relationship between growth (as total dry weight) and nitrogen content was found as well.*

Keywords: ornamental plant, peat, river waste, nitrogen

INTRODUCTION

Substrate selection is an important factor influencing plant quality and one of the critical decisions that must be made when a pot bedding plant production is started (Di Benedetto, 2011). The increasing demand of growing media for greenhouse horticultural uses and the scarcity and increasing

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cost of traditional substrates, such as those based on *Sphagnum* peat moss, have raised the interest in new substrates (Di Benedetto, 2007).

The need to develop new substrates for the horticulture industry to replace peat moss is an issue that is being addressed by researchers around the world (Chavez et al., 2008; Di Benedetto, 2007; Di Benedetto and Pagani, 2012; Jackson et al., 2009a, 2009b; Blok and Verhagen, 2009). Although some of these growing media/substrates are generally limited in quality in terms of physical and chemical properties and negatively affect the development of plant roots, several commercialized products currently available to growers have been developed (Blok and Verhagen, 2009; Jackson et al., 2010). The lack of a clear understanding of plant adaptation to different growing media and of the physiological mechanisms involved in this growth regulation limits our efforts to find a real alternative to peat moss for bedding pot plants.

The growth dynamics of short-lived plants such as bedding plants is critical because they complete their life cycle in a short time and normally do not have enough time to adjust to unfavorable environmental conditions. Thus, if they are initially grown in a less favorable condition, they have to be managed with good horticultural practices throughout the whole growth cycle. Under poor growing conditions, most bedding plants tend to flower prematurely, giving a poor quality of short-statured plants with small flowers.

Growing medium give not only a matrix for water and nutrient absorption so a source of external signaling; different plants would respond through different physiological mechanisms. The traditional approach to select new growing medium has been focused on selecting organic and inorganic materials which, as a part of a mix, allow developing an alternative to the high quality peat-based growing medium (Di Benedetto et al., 2006b; Landis and Morgan, 2009; Di Benedetto and Pagani, 2012). It has been pointed out that aeration in soilless mixes is often a problem (Caron and Nkongolo, 1999). After the partial saturation and the complete drainage of a growing medium, a very small-perched water table occurs at the bottom of the pot, resulting in a medium equilibrated at very high water potentials. Under these conditions, many of the pores of the growing medium tend to remain saturated, further increasing the risk of root asphyxia if the period of saturation of a large proportion of these pores is prolonged. Because simulation studies have shown the importance of characterizing physical properties (Beardsell et al., 1979; Fonteno, 1989), the traditional approach from growing media has been optimizing this matter.

Researchers have long tried to find a growing medium able to replace the high quality peat-based substrate (Gruda and Schnitzler, 2004; Abad et al., 2005; Perez-Murcia et al., 2005; Di Benedetto, 2007; Bustamante et al., 2008; Chamani et al., 2008; Awang et al., 2009; Di Benedetto and Pagani, 2012). The emphasis of their research was put on the particle size of the individual components.

The present research was performed under the hypothesis that a growing medium is an emissary for plant responses and that a broad range of growing media, showing different relative growth rates, would be useful to determine the physiological mechanisms involved. One of the long-distance signals mediating the shoot response is the perception of nitrate in roots, which seems to involve cytokinins (Hermans et al., 2006; Rubio et al., 2009). There are several reports suggesting that the accumulation of cytokinins is closely correlated with the nitrogen status of the plants (Takei et al., 2002). Thibaud et al. (2012) has suggested that the nitrogen signaling associated with cytokinin synthesis by roots is involved in the adaptation of *I. wallerana* plants to different growing media. The objective of this study was to describe the physiological mechanisms involved in *I. wallerana* growth when cropped on a broad range of growing media created from alternative components.

MATERIALS AND METHODS

Plant Material and Experimental Design

Different growing media were formulated using *Sphagnum maguellanicum* (**S**) and *Carex* (**C**) peat from the Southern Argentina peat lands (55°S to 52°S and 46°S to 42°S respectively), river waste ('temperate peat') (R_1: fine grade and R_2: gross grade) resulting from the accumulation of plant residues under an anaerobic environment dredged from river or lake banks (34°S to 27°15'S) and rice hull (RH) from a rice mill. A commercial high quality peat-based medium (Fafard Growing Mix 2®) (Canadian *Sphagnum* peat moss-perlite-vermiculite 70:20:10 v/v) was used as a control. The formulae (v/v) tested were:

F: Fafard Growing Mix 2®

S_2: S (80%) + RH (20%)

S_4: S (60%) + RH (40%)

S_6: S (40%) + RH (60%)

S_8: S (20%) + RH (80%)

C_2: C (80%) + RH (20%)

C_4: C (60%) + RH (40%)

C_6: C (40%) + RH (60%)

C_8: C (20%) + RH (80%)

$R_{1\text{-}2}$: R_1 (80%) + RH (20%)

$R_{1\text{-}4}$: R_1 (60%) + RH (40%)

$R_{1\text{-}6}$: R_1 (40%) + RH (60%)

$R_{1\text{-}8}$: R_1 (20%) + RH (80%)

$R_{2\text{-}2}$: R_2 (80%) + RH (20%)

$R_{2\text{-}4}$: R_2 (60%) + RH (40%)

$R_{2\text{-}6}$: R_2 (40%) + RH (60%)

$R_{2\text{-}8}$: R_2 (20%) + RH (80%)

$SR_{1\text{-}2}$: S (40%) + R_1 (40%) + RH (20%)

$SR_{1\text{-}4}$: S (30%) + R_1 (30%) + RH (40%)

$SR_{1\text{-}6}$: S (20%) + R_1 (20%) + RH (60%)

$SR_{1\text{-}8}$: S (10%) + R_1 (10%) + RH (80%)

$SR_{2\text{-}2}$: S (40%) + R_2 (40%) + RH (20%)

$SR_{2\text{-}4}$: S (30%) + R_2 (30%) + RH (40%)

$SR_{2\text{-}6}$: S (20%) + R_2 (20%) + RH (60%)

$SR_{2\text{-}8}$: S (10%) + R_2 (10%) + RH (80%)

$CR_{1\text{-}2}$: C (40%) + R_1 (40%) + RH (20%)

$CR_{1\text{-}4}$: C (30%) + R_1 (30%) + RH (40%)

$CR_{1\text{-}6}$: C (20%) + R_1 (20%) + RH (60%)

$CR_{1\text{-}8}$: C (10%) + R_1 (10%) + RH (80%)

$CR_{2\text{-}2}$: C (40%) + R_2 (40%) + RH (20%)

CR_{2-4}: C (30%) + R_2 (30%) + RH (40%)

CR_{2-6}: C (20%) + R_2 (20%) + RH (60%)

CR_{2-8}: C (10%) + R_2 (10%) + RH (80%)

I. wallerana 'Accent' seeds (Goldsmith Inc.) were germinated and grown in 200 plastic plug trays in Fafard Growing Mix 2® under greenhouse facilities located at the Faculty of Agronomy, University of Buenos Aires, Argentina (34°28'S). At the fourth true leaf stage, one plant per pot was transplanted. The 33 soilless media were tested in 1,200 cm^3 pots. The experiment was repeated twice. All the materials were limed to achieve similar pH's (5.5–5.6). Mean temperatures (25.7–26.3 °C) and photosynthetic active radiation (4.48–5.76 mol photons m^{-2} day^{-1}) for the different experiments were recorded with a HOBO sensor (H08-004-02) connected to a HOBO H8 data logger (Onset, Bourne,MA). Q2

Pots were weekly fertilized with 150 mg L^{-1} nitrogen (N) [1 N :0.5 phosphorus (P): 1 potassium (K): 0.5 calcium (Ca) wt/wt] from transplant to sale stages; the volume per pot varied according to the cation exchange capacity (CEC) of each growing medium. Plants were watered daily with tap water as needed (pH: 6.64 and electrical conductivity of 0.486 dS m^{-1}).

Data Analysis

Plants were harvested at the transplant stage and seventy days later (sale stage). Ten plants of each growing medium were separated into roots and shoots and their fresh mass determined. Plants were dried at 80°C for 48 h and weighed to obtain the dry aerial and root biomass weight. Leaf area was determined with a LI-COR 3000A automatic leaf area meter (LI-COR, Lincoln, NE, USA). The relative growth rate (RGR) was calculated as the slope of the straight-line regression of the natural logarithm of whole-plant dry mass vs. time in days whereas the relative leaf area expansion rate (RLAER) was calculated as the slope of the regression of the natural logarithm of total leaf area vs. time in days. The mean net assimilation rate (NAR), leaf area ratio (LAR), and leaf area partitioning (LAP) were calculated according to Potter and Jones (1977). Changes in allometric relationships between shoots and roots were estimated using a straight-line regression analysis between the natural logarithm root dry weight and the natural logarithm shoot dry weight.

Samples of each substrate were collected, and total porosity, air-filled porosity, density and container capacity were determined according to Fonteno (1996). Samples of air-dry media for particle size distribution were passed through a series of 25 to 2 mm sieves. Electrical conductivity (EC) and pH were analyzed in a 1:5 (v/v) water extract (Bailey, 1996). Nutrient

TABLE 1 Chemical properties of the materials used for performing the growing media tested

Growing media	pH*	EC (dS m^{-1})	N (%)	P (m mol L^{-1})	K (m mol L^{-1})	Ca (m mol L^{-1})	Mg (m mol L^{-1})	CEC (meq 100 cm^{-3})
F	5.59*b*	0.41*c*	1.68	9.92*a*	0.08*b*	1.30*a*	0.29*b*	7.99*b*
S	3.89*c*	1.16*b*	0.93	1.50*c*	0.08*b*	0.72*b*	0.21*b*	4.57*c*
C	4.12*c*	3.05*a*	1.10	3.10*b*	0.03*b*	0.92*b*	0.19*c*	4.84*c*
R	5.15*b*	1.02*b*	1.16	3.09*b*	0.36*a*	0.86*b*	0.40*a*	13.30*a*
RH	6.77*a*	0.48*c*	0.65	1.55*c*	0.02*b*	0.37*c*	0.14*c*	1.03*d*

F (Canadian *Sphagnum* peat), S (*Sphagnum maguellanicum* peat), C (*Carex* peat), R (River waste), RH (rice hull).

* Initial pH before limed adjustment.

Mean values (n = 3) followed by a different lower-case letters were significantly different at $P < 0.05$ by Tukey's test.

concentration analysis included: nitrogen (Kjeldahl method), phosphorus (colorimetrically), potassium, calcium and magnesium (atomic absorption). The cation-exchange capacity (CEC) was determined with 1 M ammonium acetate at pH = 7. Chemical analyses were performed in triplicate and physical analyses included five samples.

Statistical Analysis

The experiment had a randomized complete block design with 10 single-pot replications of each growing medium tested. Since there were no significant differences between the two experiments, they were considered together. Data were subjected to a one-way analysis of variance and means were separated by Tukey's test ($P < 0.05$).

RESULTS

The chemical properties of the control substrate (F) and the components of the growing media tested are shown in Table 1. Both Argentinean peats, *Sphagnum maguellanicum* (S) and *Carex sp.* (C) showed a very low pH value and needed a pH adjustment using dolomite loam previous to use. Electrical conductivity (EC) was very low for both the control substrate (F) and rice hull (RH), whereas river waste (R) and both Argentinean peat treatments especially *Carex sp.* (C), showed higher EC values. The nutrient concentrations of the growing media tested were quite different from those the control substrate (F). The control substrate (F) showed the highest nitrogen and phosphorus concentrations. Treatment R showed the highest potassium values whereas there were no differences in the calcium and magnesium concentrations between the control substrate (F) and the alternative materials tested. The highest CEC was associated with the river waste component. Different mixes from these alternative materials gave a wide range of chemical properties (data not shown).

The proportion of particle sizes was analyzed at the beginning and at the end of the experiments 70 days later. While at the beginning of the experiments, the control (F) concentrated the highest proportion of particles in the two smaller size categories, the rest of the growing media tested showed a variable, but important proportion, of particles of higher sizes. The control substrate (F) showed slight changes in particle size at the end of the experiments (70 days later) whereas the remaining growing media had a decreased proportion of higher particle sizes (Table 2).

Total porosity of many growing media at the beginning of the experiments was either similar to or higher than that of the control substrate (F) at the end of the experiments (70 days later) (Figure 1a). The initial air-filled porosity was also lower for the control substrate than for the remaining growing media tested and when the proportion of rice hull in the mixes increased in the material, high air-filled porosity was recorded. The final air-filled porosity values of most of the growing media tested, except in the mixes receiving a high proportion of rice hull, was below that of the control substrate (F) (Figure 1b). Mixes with river waste showed higher density than the control substrate (F) and the mixes including *Sphagnum maguellanicum* or *Carex sp.* and rice hull (Figure 1c). The control substrate (F) had the highest initial and final container capacity compared to many of the growing media tested (Figure 1c).

The highest *I. wallerana* aerial fresh weight was achieved by the control substrate (F) and treatments $R_{1\text{-}2}$ and $SR_{1\text{-}2}$. At the end of the experiments the root fresh weight of many growing media was either equal to or higher than that of the control (F) (Figure 2).

Total dry weight was related to the initial particle size lower than 2 mm; the determination coefficient r^2 was 0.645 (Figure 3). On the other hand, Figure 4 shows that there was a close relationship ($r^2 = 0.809$) between shoot and root dry weight.

The highest RLAER was found only in three growing media: the control substrate (F), the river waste ($R_{1\text{-}2}$) and the mix of *Sphagnum magellanicum* and river waste ($SR_{1\text{-}2}$). The highest RGR was found in these three growing media and in two additional mixes of *Sphagnum magellanicum* and river waste ($SR_{1\text{-}4}$ and $SR_{1\text{-}6}$). However, some other mixes showed slightly lower RGRs. The coefficients of determination r^2 of the straight-line regression analysis between the natural logarithm of total dry weigh and days ranged from 0.802 to 0.979 (data not shown). The lowest RGR values were associated with a decrease in both NAR and LAR. The mixes with lowest RGRs also showed a decrease in LAP (Table 3). The coefficients of determination (r^2) of the straight-line regression analysis between the natural logarithm of the total leaf area and days used for RLAER, NAR, LAR and LAP calculations ranged from 0.717 to 0.982 (data not shown).

TABLE 2 Particle size distribution (%) from the different growing media used at the beginning of the experiments (Initial) and at the sale stage (final) from the *I. wallerana* bedding plants grown during 70 days in pots. Growing media abbreviations are as in Figure 1

	Particle size (mm)											
	Initial						Final					
	>24.50<	>12.70<	>6.35<	>4.80<	>2.00<	<2.00	>24.50<	>12.70<	>6.35<	>4.80<	>2.00<	<2.00
F	0.00	1.48	6.99	4.86	36.85	49.82	0.00	0.76	4.41	3.15	41.85	49.83
S-2	0.00	8.91	10.68	3.10	34.18	43.13	0.00	5.90	11.57	2.10	35.20	45.23
S-4	2.33	6.80	9.67	2.31	44.33	34.56	0.00	4.43	6.45	2.24	49.50	37.38
S-6	0.00	6.39	7.42	1.51	62.13	22.55	0.00	2.95	6.79	1.27	56.44	32.55
S-8	0.00	1.12	3.50	1.23	76.92	17.23	0.00	0.39	3.10	1.12	77.41	17.98
C-2	2.01	36.74	9.10	6.52	22.53	23.10	1.69	21.50	23.29	15.70	13.82	24.00
C-4	0.00	8.90	29.00	6.60	39.00	16.50	0.00	6.50	16.94	3.97	50.24	22.35
C-6	0.00	12.07	5.60	7.07	60.33	14.93	0.00	5.69	9.22	1.95	57.81	25.33
C-8	0.00	1.50	1.33	10.32	61.85	25.00	0.00	0.90	0.81	1.70	61.59	35.00
$R_{1\text{-}2}$	0.00	6.72	13.30	4.70	50.72	25.20	0.00	0.00	2.88	3.72	55.20	38.20
$R_{1\text{-}4}$	0.00	3.00	5.53	1.44	49.70	40.33	0.00	0.00	3.90	3.80	42.87	49.43
$R_{1\text{-}6}$	0.00	3.92	8.90	0.89	69.28	17.01	0.00	0.00	0.00	3.26	61.82	34.92
$R_{1\text{-}8}$	0.00	0.94	7.20	0.68	71.73	19.45	0.00	0.00	0.63	14.46	57.37	27.54
$R_{2\text{-}2}$	0.30	8.00	24.05	13.78	28.82	18.49	0.00	5.52	15.70	17.30	18.65	42.83

$R_{2\text{-}4}$	0.00	15.70	19.65	7.41	28.20	29.04	0.00	6.00	16.28	4.30	32.64	40.78
$R_{2\text{-}6}$	0.00	7.86	11.30	3.31	57.10	20.43	0.00	6.00	8.96	4.00	53.61	27.43
$R_{2\text{-}8}$	3.10	2.47	7.90	1.44	63.60	21.49	0.00	1.94	8.26	1.11	67.86	20.83
$SR_{1\text{-}2}$	0.00	1.42	6.56	1.90	34.70	55.42	0.00	1.37	3.43	2.17	19.80	73.23
$SR_{1\text{-}4}$	0.00	2.46	4.40	1.90	40.30	50.94	0.00	2.19	3.20	1.58	38.50	54.53
$SR_{1\text{-}6}$	0.00	3.00	5.00	0.97	46.37	44.66	0.00	2.80	3.10	2.10	47.00	45.00
$SR_{1\text{-}8}$	0.00	0.69	1.42	0.37	71.30	26.22	0.00	0.00	0.01	0.60	61.36	38.03
$SR_{2\text{-}2}$	1.39	1.80	9.80	0.80	53.30	32.91	0.00	0.10	4.10	4.80	43.79	47.21
$SR_{2\text{-}4}$	1.36	6.00	10.63	0.45	53.77	27.79	0.00	1.36	0.14	4.30	45.56	48.64
$SR_{2\text{-}6}$	1.10	5.90	9.96	3.10	41.64	38.30	0.00	1.90	7.50	3.80	44.30	42.50
$SR_{2\text{-}8}$	0.00	1.10	7.32	3.25	43.00	45.33	0.00	0.00	4.60	1.29	48.60	45.51
$CR_{1\text{-}2}$	0.00	7.40	11.20	2.20	26.72	52.48	0.00	0.01	2.76	1.61	25.90	69.72
$CR_{1\text{-}4}$	2.60	6.29	13.76	1.76	40.94	34.65	0.00	3.38	11.10	4.20	39.51	41.81
$CR_{1\text{-}6}$	1.84	1.11	6.56	3.59	57.00	29.90	0.00	0.57	4.10	0.83	59.84	34.66
$CR_{1\text{-}8}$	0.00	2.34	7.58	6.88	61.10	22.10	0.00	2.43	1.81	1.30	60.40	34.06
$CR_{2\text{-}2}$	0.00	11.50	21.42	4.10	24.70	38.28	0.00	7.11	15.88	5.85	29.60	41.56
$CR_{2\text{-}4}$	0.00	9.63	14.15	5.70	39.78	30.74	0.00	4.12	14.25	1.30	38.40	41.93
$CR_{2\text{-}6}$	0.00	9.05	14.90	2.19	48.54	25.32	0.00	8.40	10.26	2.58	50.47	28.29
$CR_{2\text{-}8}$	0.00	3.33	6.10	0.83	66.00	23.74	0.00	1.10	4.92	2.68	59.73	31.57

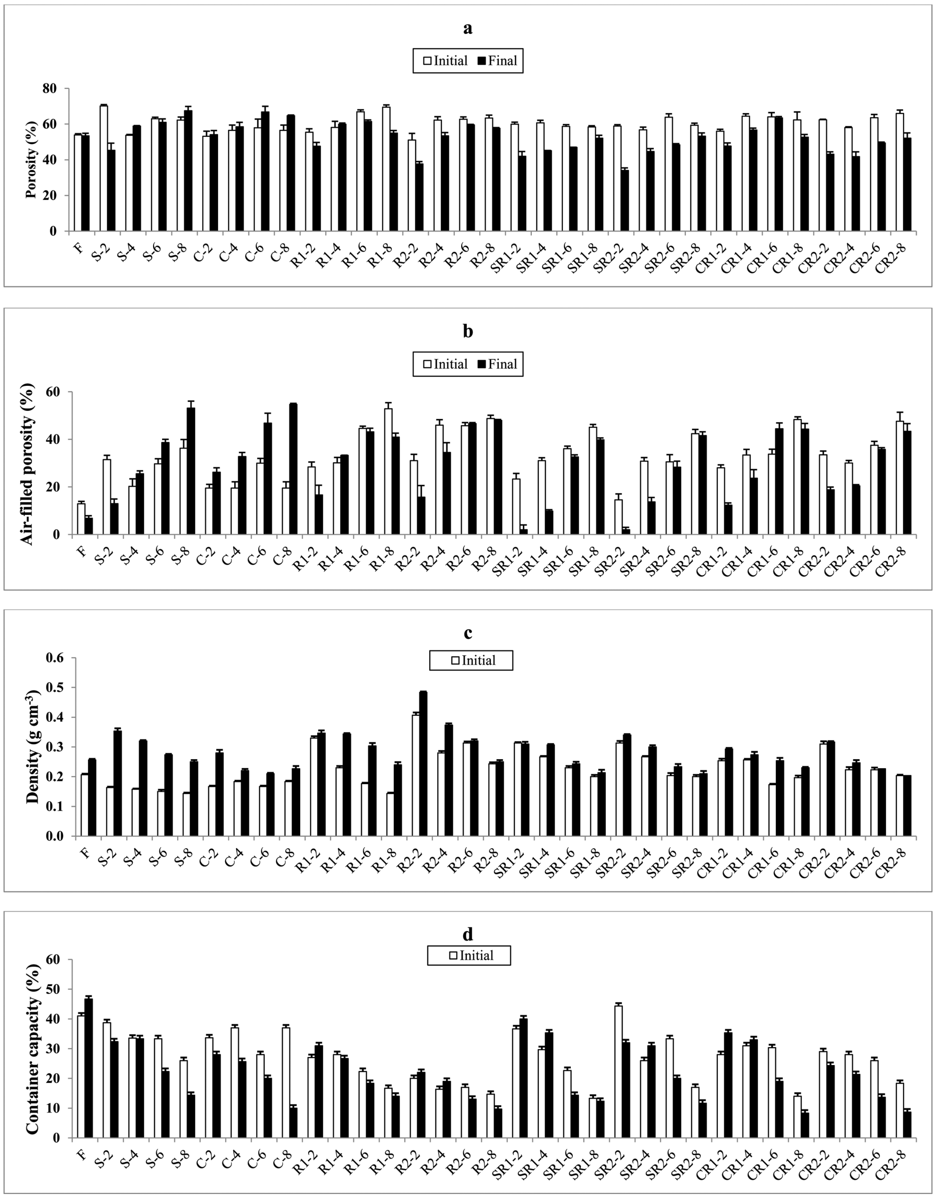

FIGURE 1 Changes in porosity A) and air filled-porosity B), density C) and container capacity D) for plants of *Impatiens wallerana* grown in different substrates between the beginning (transplant stage) and the end (sale stage) of the experiments. The standard errors are indicated. F (control substrate), S (*Sphagnum maguellanicum* peat), C (*Carex* peat), R (river waste). SR [*Sphagnum maguellanicum* peat + river waste (v/v)], CR [*Carex* peat + river waste (v/v)], SC [*Sphagnum maguellanicum* peat + *Carex* peat (v/v)]. R_1 (river waste, fine grade), R_2 (river waste, gross grade). -2, -4, -6 and -8 indicate 20%, 40%, 60% and 80% rice hull in the mix.

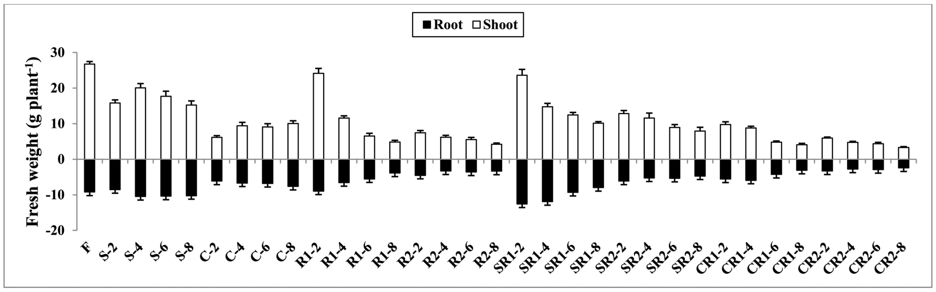

FIGURE 2 Fresh weight roots and shoots at the end of the experiments for plants of *I. wallerana* grown in different growing media. The standard errors are indicated. Growing media abbreviations are as in Figure 1.

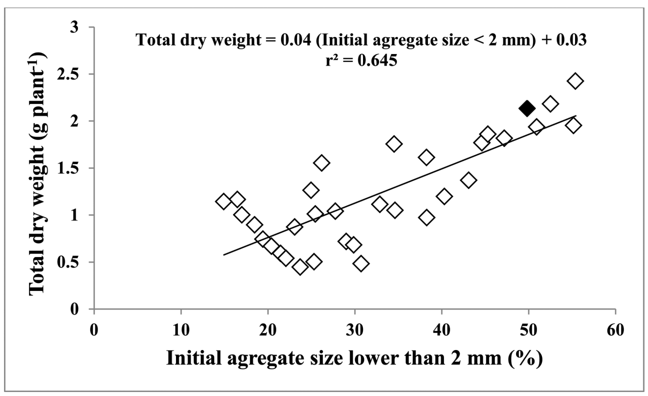

FIGURE 3 Straight-line regressions between total dry weights vs. initial aggregate size lower than 0.2 mm proportion for *I. wallerana* plants grown on different growing media at the sale stage. ◇: F (Control substrate).

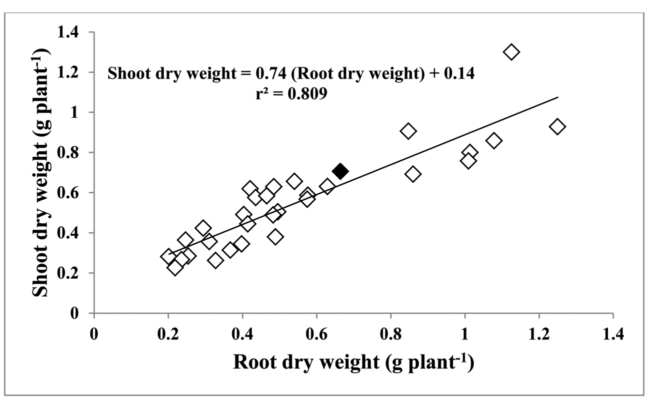

FIGURE 4 Straight-line regressions between shoot vs. root (on a dry weight base) for *I. wallerana* plants grown on different growing media at the sale stage. ◇: F (Control substrate).

TABLE 3 Changes in relative leaf area expansion rate (RLAER), relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (NAR) and leaf area partitioning (LAP) for plants of *I. wallerana* grown in different growing media. The standard errors for RLAER and RGR are indicated. Growing media abbreviations are as in Figure 1

Growing media	RLAER $cm^2\ cm^{-2}\ day^{-1}$	RGR $g\ g^{-1}\ day^{-1}$	NAR $g\ cm^{-2}\ day^{-1}$ (x 10^{-5})	LAR $cm^2\ g^{-1}$	LAP $\frac{cm^2\ day^{-1}}{g\ day^{-1}}$
F	0.049 ± 0.0013	0.048 ± 0.0018	41.97	115.14	116.96
S-2	0.037 ± 0.0020	0.038 ± 0.0016	33.14	113.31	112.61
S-4	0.042 ± 0.0016	0.043 ± 0.0012	38.79	109.58	107.14
S-6	0.041 ± 0.0014	0.045 ± 0.0018	42.54	105.53	96.03
S-8	0.039 ± 0.0015	0.043 ± 0.0017	42.62	100.20	88.68
C-2	0.024 ± 0.0018	0.031 ± 0.0018	32.58	94.87	72.33
C-4	0.031 ± 0.0017	0.037 ± 0.0017	37.61	97.48	82.20
C-6	0.030 ± 0.0019	0.036 ± 0.0017	36.84	97.04	80.63
C-8	0.031 ± 0.0017	0.036 ± 0.0017	35.82	10.40	87.23
R_{1-2}	0.047 ± 0.0014	0.047 ± 0.0024	44.04	10.83	106.87
R_{1-4}	0.014 ± 0.0017	0.039 ± 0.0024	41.33	94.59	83.55
R_{1-6}	0.035 ± 0.0016	0.035 ± 0.0024	41.39	85.28	61.96
R_{1-8}	0.026 ± 0.0019	0.031 ± 0.0027	35.90	85.31	58.50
R_{2-2}	0.021 ± 0.0023	0.032 ± 0.0016	33.52	96.42	79.27
R_{2-4}	0.027 ± 0.0016	0.029 ± 0.0016	28.78	99.42	82.94
R_{2-6}	0.024 ± 0.0014	0.028 ± 0.0020	28.24	98.22	78.66
R_{2-8}	0.022 ± 0.0021	0.026 ± 0.0018	27.52	94.60	68.33
SR_{1-2}	0.019 ± 0.0020	0.051 ± 0.0025	49.02	104.85	98.82
SR_{1-4}	0.049 ± 0.0023	0.047 ± 0.0021	46.85	99.31	86.87
SR_{1-6}	0.041 ± 0.0023	0.045 ± 0.0018	47.98	93.29	77.67
SR_{1-8}	0.037 ± 0.0018	0.042 ± 0.0016	48.33	86.81	67.11
SR_{2-2}	0.032 ± 0.0017	0.040 ± 0.0028	36.47	109.03	106.07
SR_{2-4}	0.039 ± 0.0024	0.038 ± 0.0030	34.97	108.39	104.11
SR_{2-6}	0.036 ± 0.0028	0.035 ± 0.0022	33.82	102.22	90.54
SR_{2-8}	0.031 ± 0.0022	0.031 ± 0.0021	30.68	102.25	88.32
CR_{1-2}	0.027 ± 0.0025	0.036 ± 0.0025	35.54	102.24	92.44
CR_{1-4}	0.033 ± 0.0022	0.037 ± 0.0020	38.55	95.01	79.72
CR_{1-6}	0.031 ± 0.0017	0.030 ± 0.0024	32.36	92.51	68.88
CR_{1-8}	0.022 ± 0.0025	0.022 ± 0.0028	22.46	97.84	73.31
CR_{2-2}	0.016 ± 0.0023	0.028 ± 0.0023	28.22	100.64	87.71
CR_{2-4}	0.025 ± 0.0020	0.024 ± 0.0022	24.00	100.69	85.53
CR_{2-6}	0.021 ± 0.0017	0.025 ± 0.0024	25.78	95.88	74.52
CR_{2-8}	0.019 ± 0.0020	0.021 ± 0.0018	22.68	94.22	63.59

Table 4 shows the changes found in allometric relationships between shoots and roots for *I. wallerana* plants grown in different growing media. The slopes of the straight lines which related the natural logarithm of root dry weight and the natural logarithm of shoot dry weight showed that plants grown in the control substrate (F) assigned a higher photo-assimilated proportion to shoot growth while in the rest of growing media the plants partitioned a higher photosynthate proportion to roots. The coefficients of determination (r^2) ranged from 0.834 to 0.977.

TABLE 4 Changes in allometric relationships between shoots and roots for *I. wallerana* plants grown in different growing media using a lineal straight line regression analysis between natural logarithm root dry weight and natural logarithm shoot dry weight. The standard errors for the straight- light regression slopes (β) are indicated. The intercept straight-line (α) and the coefficients of determination r^2 are indicated too. Growing media abbreviations are as in Table 3. Growing media abbreviations are as in Figure 1

	Transplant-Sale stage		
Growing media	α	β	r^2
F	−0.578	0.789 ± 0.035	0.947
S-2	−0.194	0.950 ± 0.044	0.942
S-4	−0.073	0.978 ± 0.038	0.962
S-6	0.017	1.036 ± 0.058	0.918
S-8	0.113	1.059 ± 0.058	0.952
C-2	0.060	1.039 ± 0.046	0.877
C-4	−0.039	0.983 ± 0.074	0.929
C-6	0.004	0.999 ± 0.051	0.943
C-8	−0.121	0.963 ± 0.046	0.935
$R_{1\text{-}2}$	−0.281	0.894 ± 0.053	0.936
$R_{1\text{-}4}$	−0.062	0.961 ± 0.044	0.867
$R_{1\text{-}6}$	0.127	1.042 ± 0.071	0.922
$R_{1\text{-}8}$	0.327	1.116 ± 0.057	0.912
$R_{2\text{-}2}$	−0.278	0.902 ± 0.065	0.922
$R_{2\text{-}4}$	−0.537	0.808 ± 0.050	0.900
$R_{2\text{-}6}$	−0.374	0.862 ± 0.051	0.918
$R_{2\text{-}8}$	−0.015	0.984 ± 0.050	0.838
$SR_{1\text{-}2}$	−0.147	0.959 ± 0.085	0.977
$SR_{1\text{-}4}$	0.014	1.018 ± 0.028	0.953
$SR_{1\text{-}6}$	0.129	1.059 ± 0.044	0.959
$SR_{1\text{-}8}$	0.102	1.049 ± 0.042	0.951
$SR_{2\text{-}2}$	−0.294	0.900 ± 0.051	0.960
$SR_{2\text{-}4}$	−0.414	0.856 ± 0.035	0.950
$SR_{2\text{-}6}$	−0.099	0.972 ± 0.037	0.963
$SR_{2\text{-}8}$	−0.268	0.919 ± 0.063	0.889
$CR_{1\text{-}2}$	−0.308	0.892 ± 0.046	0.930
$CR_{1\text{-}4}$	−0.166	0.935 ± 0.049	0.927
$CR_{1\text{-}6}$	−0.066	0.969 ± 0.064	0.898
$CR_{1\text{-}8}$	−0.327	0.887 ± 0.059	0.922
$CR_{2\text{-}2}$	0.258	1.071 ± 0.072	0.889
$CR_{2\text{-}4}$	−0.023	0.962 ± 0.081	0.834
$CR_{2\text{-}6}$	−0.120	0.946 ± 0.058	0.907
$CR_{2\text{-}8}$	−0.125	0.935 ± 0.084	0.845

Plants of *I. wallerana* grown in the control substrate (F) and river waste accumulated the highest proportion of nitrogen in shoots, whereas, plants grown in *Sphagnum maguellanicum*- and *Carex* sp-based substrates increased nitrogen accumulation in roots related to shoots (Figure 5a). The straight lines which related nitrogen content and final fresh weight showed a close relationship but significantly higher for shoots ($r^2 = 0.796$) than for roots ($r^2 = 0.535$) (Figure 5b).

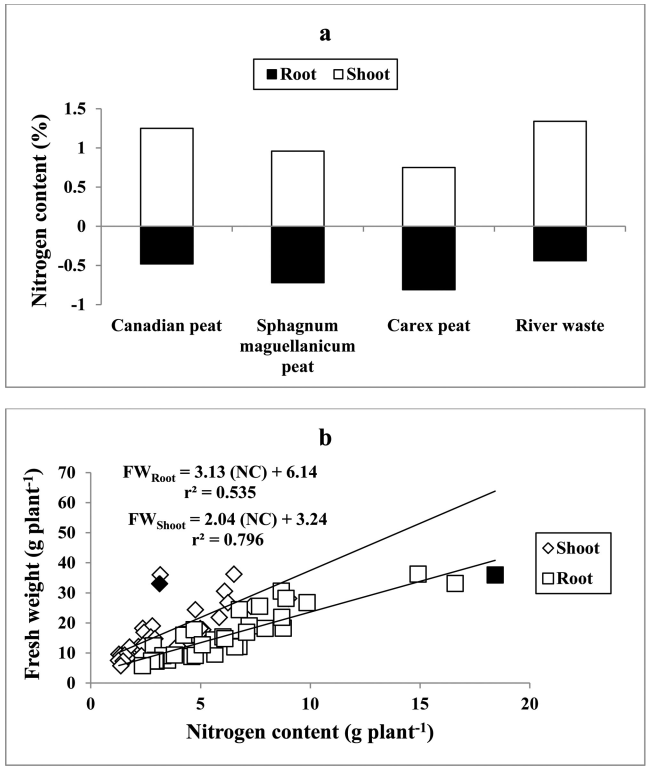

FIGURE 5 Nitrogen distribution between A) roots and shoots and b) the fresh weight-nitrogen content relationships for *I. wallerana* plants grown on different growing media. ◇: F (Canadian peat): [Canadian *Sphagnum* peat (80%) + Perlite (10%) + Vermiculite (10%)]. *Sphagnum maguellanicum* peat: [S_2: S (80%) + RH (20%)]; Carex peat: [C_2: C (80%) + RH (20%)] and river waste: [$R_{1\text{-}2}$: R (80%) + RH (20%)].

DISCUSSION

The materials used to obtain the thirty mixes tested in this study had been previously tested individually as a growing medium showing that they can partially replace peat (Chavez et al., 2008; Di Benedetto et al., 2006b; Di Benedetto and Pagani, 2012). Thus, here a broad range of mixes with both high porosity (Figure 1a) and air-filled porosity (Figure 1) was developed. At the same time, the container capacity (Figure 1d) and cation exchange capacity (Table 1) were used to program water and fertilization routines. As a result, fresh weight at the sale stage (70 days from the beginning of the experiments) showed significant differences among the growing media tested (Figure 2).

One of the most important considerations in formulating a growing medium, regardless of the materials used, is the particle size of the individual components. Particle size largely determines the physical properties (total porosity, air-filled porosity, bulk density and container porosity) of the medium (Noguera et al., 2003; Bilderback et al., 2005). Since each component has a different particle density and a different particle size, there can be unexpected results (Thibaud et al., 2012). Table 2 shows that the differences in the physical properties between the control substrate (F) and the different mixes tested would be associated with changes in the proportion of pore sizes between the beginning and the end of the experiments, 70 days later. The decrease in large particles and the increase in fine particles during the experiments as an evidence of substrate breakdown are in agreement with the results by Bilderback et al. (2005).

Ornamental plants grown in pots may show a well-developed root system with white roots and without damage but with a horizontal root growth around the pot, root growth restrictions often occur (Di Benedetto and Klasman, 2004; Di Benedetto, 2011; Di Benedetto et al., 2006a). The cytokinins synthesized in the root apex and reallocated to shoots would decrease when the vertical root growth was impeded by the container base. There is strong evidence that cytokinins are root factors, which are transported via the xylem to the shoot, where they exert a major regulatory influence on growth and photosynthesis (Chernyad'ev, 2005; Santner et al., 2009). Since the rooting volume of a potted plant is very restricted, one important requirement of soilless potting substrates is that they must have considerable water holding capacity and air-filled porosity; the latter was not true for *I. wallerana* growth in alternative growing media with a high proportion of rice hull (Figure 1b vs. Figure 2). Plant roots can sense adverse soil conditions and, via some internal signal, transmit the condition of the soil to extending leaves, with the typically net result of a decrease in leaf elongation rates (Doerner, 2007).

Plants increases biomass production through both the appearance of shoots and the expansion of leaves. The size of the different plant sinks determines the partition of photo-assimilates to each plant organ. Figure 4shows that shoot fresh weight was mainly determined by the size of root system ($r^2 = 0.809$), in agreement with close coordination between root and shoot growth controlled by a signaling pathway, which is largely hormonal with a major site of control located in the root system (De Vries and Dubois, 1990; Hirose et al., 2008). It has been indicated that increased root growth may lead to an increase in the synthesis of cytokinins (O'Hare and Turnbull, 2004); exogenous cytokinin supply to ornamental pot plants favors the development of shoots and tends to increase leaf biomass (Zieslin and Algom, 2004; Di Benedetto, 2011; Di Benedetto et al., 2010, 2013; De Lojo and Di Benedetto, 2014). However, neither crop productivity in ornamental plants nor the mechanisms involved in plant response to exogenous cytokinins supply under commercial facilities have been well studied yet and are the matter for future research.

Figure 4also shows a close relationship ($r^2 = 0.645$) between *I. wallerana* growth (expressed as dry weight accumulation) and fine particle size for the growing media tested. Although the highest RGR was found in the control substrate (F) and a few alternative mixes, Table 3 shows that there were only slight differences with the remaining growing media tested. However, in petunia and pansy, Di Benedetto et al. (2006b) showed that many alternative growing media fail to lead to high plant quality (leaf area, plant height and flower number), plant growth and aerial plant productivity. When RGR was disaggregated as the product of NAR and LAR, a decrease both in the "physiological component" and in the "morphological component" for the lowest RGR values was found. The mechanism involved would be associated with a change in photosynthate partitioning, which favors root growth, as shown in plant allometries from Table 4and LAP shown in Table 3.

Plant organs interact with each other to optimize both metabolic and developmental processes to allow the organism to accommodate to the environment. For these mutual interactions, local and long-distance communication among cells and organs are essential (Kudo et al., 2010). Molecular genetics evidences demonstrate that roots sense and respond to local and global concentrations of inorganic nitrate, in a fashion that depends on the shoot nutrient status. Nitrate availability and distribution impact on the nitrate control of the root system architecture (Desnos, 2008). Thibaud et al. (2012) have suggested that the nitrogen signaling associated with cytokinin synthesis by roots would be involved in the *I. wallerana* plants adaptation to different growing media. Plants of *I. wallerana* grown in the control (F) and river waste-based growing media accumulated the highest proportion of nitrogen in shoots, whereas, plants grown in *Sphagnum maguellanicum*- and *Carex* sp-based substrates increased nitrogen accumulation in roots related to shoots (Figure 5a).

A key concept underpinning current understanding of the carbon/nitrogen interaction in plants is that the capacity for nitrogen assimilation is related to nutrient availability and requirements by the integrated perception of signals from hormones, nitrate, sugars, organic acids, and amino acids. Studies on the nature and integration of these signals have revealed a complex network which interplays with carbon and nitrogen signals (Hwang and Sakakibara, 2006; Hirose et al., 2008; Kudo et al., 2010). These controls not only act to orchestrate the relative rates of carbon and nitrogen assimilation and carbohydrate and amino acid production, but also have a significant influence on plant development. The signal transduction network that coordinates information from carbohydrate metabolism and nitrogen assimilation is under phytohormone regulation (Foyer et al., 2003; Hermans et al., 2006; Rubio et al., 2009). Several reports have suggested that the accumulation of cytokinins is closely correlated with the nitrogen status of the plants (Takei et al., 2002). This study suggested that cytokinin metabolism and translocation could be modulated by the nitrogen nutritional status. Namely, cytokinin accumulation and translocation occurred after sensing a change in nitrogen availability. Figure 5a shows that that there is a close relationship between growth (as total dry weight) and nitrogen content, which would be in agreement with this previous information. Since the alternative growing media tested (mainly the *Sphagnum maguellanicum*- and the *Carex sp.*-based one) changed the proportion of nitrogen in the shoots (Figure 5b), may be hypothesize that the decrease in shoot growth associated with this endogenous signal. However, this investigation line needs additional experiments, which are already in progress.

CONCLUSION

Some researchers have suggested an 'ideal growing medium' based on the physical and chemical substrate properties and present research has shown that there are no correlations between plant growth and these parameters. On the other hand, pore distribution and pore stability are closely associated with the plant response and the aerial plant productivity would be controlled by the extension and functionality of the root system signals related to cytokinins synthesized by the root apexes. This is also associated with the availability of macronutrients (mainly nitrogen) and its interactions with the synthesis and translocation of cytokinins to shoot apex. In summary, an increase in the efforts to understand the physiological mechanisms related to endogenous signaling involved in plant growth will allow changing the soil-based paradigm to create better non- peat-based growing media to optimize bedding pot plant growth and productivity.

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