Micropropagation has become an important method of propagating horticultural plants (Chu and Kurtz, 1990). Transferring micropropagated plants from tubes to ex vitro conditions is normally difficult, because they have a poorly developed cuticle (Wetzstein and Sommer, 1982), functionally impaired stomata (Lee and Wetzstein, 1988), and a poorly developed root system (Pierik, 1987). Various studies have been conducted to improve the environmental conditions either in vitro or ex vitro to reduce the stressful passage to controlled exterior conditions (Desjardins et al., 1987, 1990; Donnelly et al., 1985; Lee and Wetzstein, 1988; Vanderschaeghe and Debergh, 1987; Wetzstein and Sommer, 1982, 1983).

Vesicular-arbuscular mycorrhizal (VAM) fungi can form a symbiosis with a wide variety of plant hosts. Beneficial interactions between VAM fungi and horticultural crops have been well documented (Menge, 1983). The symbiosis stimulates growth and development of plants (Biermann and Linderman, 1983; Crews and Johnson, 1978; Plenchette et al., 1982), increases absorption of plant immobile elements (Ames et al., 1983; Mosse, 1973), increases drought tolerance (Augé et al., 1986; Bolgiano et al., 1983), and reduces disease incidence (Dehne, 1982). Moreover, colonization with VAM fungi increases uniformity and reduces mortality (Biermann and Linderman, 1983) and injury of transplants (Menge et al., 1978). However, little is known about how VAM fungi improve acclimatization and growth of micropropagated plantlets (Granger et al., 1982; Ponton et al., 1990).

The nature and properties of substrates are critical for establishment and performance of VAM fungi and micropropagated plantlets during acclimatization. Peatmoss-based substrates are commonly used in horticultural productions in containers and have a great commercial potential as acclimatization media for micropropagated ornamentals (Castle and Ferguson, 1982). Gramam and Timmer (1984) reported that high organic-matter content and available P (>20 mg P/g substrate) in a peat-based medium inhibited mycorrhizal colonization and limited growth response of host plants. Caron and Parent (1987) further stated that the spread and efficiency of VAM fungi as well as host plant growth could be affected by the nature of the peatmoss used. Ponton et al. (1990) suggested that a brown peat-based medium was more suitable for VAM fungi (G. intraradices and G. vesiculiferum) activity and fern (Nephelepsis exaltata) growth than a black peat-based medium. But, little has been known about the effects of different types of peat-based media on VAM activity or on micropropagated plantlet acclimatization and growth.

For these reasons, a study was undertaken 1) to determine whether the mycorrhizal fungi G. intraradices and G. vesiculiferum can establish symbioses with micropropagated plants of Gerbera, Nephrolepis, Syngonium; 2) to evaluate the effects of different peat-based substrates (PBS) on VAM fungi establishment and VAM-inoculated peat-based media on acclimatization of micropropagated plants; and 3) to evaluate long-term benefits of VAM on growth and productivity of micropropagated ornamental plants.

Materials and Methods

Micropropagated plantlets. Three species of micropropagated ornamentals were used in the experiment: Gerbera jamesonii ‘Terra Mix’, Nephrolepis exaltata ‘Florida Ruffles’, and Syngonium podophyllum ‘White Butterfly’. The explants were surface disinfested for 2 min with 70% ethanol, 30 min in 1.5%...
sodium hypochlorite with 0.01% Tween-20, followed by four 5-
min rinses in sterilized distilled water. The basal nutrient medium 
in all experiments contained Murashige and Skoog (1962) salts 
and vitamins (MS), 3% sucrose, and 0.7% Difco Bacto agar. The pH 
was adjusted to 5.7 with 0.1 N NaOH. The concentration of plant 
growth regulators in the medium was (in µM) 23.2 kinetin 
(N6·furfuryladenine) + 2.9 IAA (indole-3-acetic acid) for Ger-
bera, 9.3 kinetin + 0.05 NAA (α—naphthaleneacetic acid) for Nep-
phrolepis, and 13.3 BA (6-benzyladenine) + 1.6 NAA for Syn-
gonium. The cultures were incubated at a constant 24 ± 2C, 
under a 16-h photoperiod provided by fluorescent lamps (cool-
white) supplying 48 µmol·s−1·m−2 photosynthetic photon flux (PPF). 
Following 6 monthly subcultures, 500 micropropagated plantlets 
per species were obtained for the experiments.

Substrates. The substrates used in the experiments were peat-
based and were prepared by Tourbières Premier (Rivière-du-
Loup, Québec, Canada). Three PBS were prepared by combining 
(v/v) 1 vermiculite (fine grind no. 2) : 3 moss peat. Substrate 1 was 
a fibric-mesic sphagnum peatmoss, sifted through a 19-mm mesh 
sieve, with a decomposition value of H4 on the Von Post scale. 
This substrate is fine-textured and is similar to a germination 
medium sold commercially by the company. Substrate 2 was 
finely ground (5-mm) fabric sphagnum peat moss peat, with a 
decomposition value of H2 on the Von Post scale. Substrate 3 was 
a fibric peat moss peat, also with a decomposition value of H2. The 
three substrates differed in their physical and chemical character-
istics (Table 1).

VAM inocula. The Glomus intraradices and G. vesiculiferum 
used were commercial VAM inocula produced by Centre de Recherche Premier (Rivière-du-Loup). Samples of these two Glo-
mus species have been deposited at the National Mycology Her-
barium, Ottawa, Canada, and are respectively identified with the numbers DAOM 197198 and DAOM 198351. The three substrates 
were inoculated with either G. intraradices or G. vesiculiferum or 
were not inoculated and used as controls. The substrates were not 
stereilized. A priori, all peat types were devoid of VAM fungi as 
confirmed by the absence of colonization with the noninoculated 
treatments. Experimental substrates were inoculated by adding a 
liter mixture of leek (Allium amelo-prasum L.) roots pieces and 
inoculated substrate containing spores and hyphae of the appropri-
te fungus into 113 liters of peat substrate. Each of the two types of 
inoculated controls received the same quantity of non-mycor-
rhizal root leek.

Plant acclimatization and greenhouse conditions. The experi-
ment was conducted in a greenhouse of the Horticulture Research 
Center at Laval Univ. In vitro plantlets were transferred from test 
tubes to Cell Pack multicell containers; cell volume was 100 cm3. 
Plantlets were then grown under a small plastic tunnel and misted 
twice daily during the first 2 weeks to maintain a saturated 
air humidity. The inside of the tunnel was maintained at 23 ± 1.5C 
during the day and 20 ± 2C at night. Substrate hydration was 
maintained above 85% of full saturation. Depending on the spe-
cies, plantlets were acclimatized for an additional 2 to 4 weeks by 
gradually reducing relative humidity (RH) to the greenhouse level 
of 70% RH. Plantlets were then transferred to 100- or 125-mm-
diameter (2.3- or 2.5-liter) plastic pots containing the same sub-
strate and placed in a greenhouse. Plants were watered as needed 
and fertilized weekly with 100 ml of a solution that contained (in 
mg·liter−1) 480 MgSO4·7H2O, 750 Ca(NO3)2·4H2O, 31.4 10N-
52P2O7·10K2O (Plant Products Co., Bramalea, Ont., Canada), and 
550 12N·O5P2·44K2O (Plant Products Co.). This nutrient solu-
tion was based on that of Long Ashton (Hewitt, 1966) and is low in P.

Design of experiment. A randomized complete block design 
was used to investigate the effect of VAM and PBS on acclimati-
ization and growth of Gerbera, Nephrrolepis, and Syngonium. For 
each species, there were nine treatments consisting of a factorial 
arrangement of two VAM-inoculated treatments and a control 
noninoculated treatment, and three PBS. There were 36 plants per 
treatment randomly distributed to three blocks. Each experimental 
unit consisted of 12 plants.

Measurement and statistical analysis. The plants of each treat-
ment in each block were harvested 4, 8, 12, and 16 weeks following 
inoculation to determine the percentage of root-length coloniza-
tion. The root system was lightly washed with running tap water. 
Five root segments per plant and 15 root segments per treatment 
were sampled, and five observation points per root segment were 
examined. The percentage of root segments containing hyphae, 
arbuscules, and vesicles were determined using the grid intercept 
method of Giovannetti and Mosse (1980), after clearing and 
staining the roots with fuchsin acid according to Phillips and 
Hayman (1970). Microscopic examination was made under 125× 
magnification. The survival of plantlets was measured 4 and 8 
weeks after their transfer to ex vitro conditions and inoculation 
with mycorrhizal substrate. Growth was measured by harvesting 
three plants of each treatment in each block at 4, 8, 12, and 16 
weeks following inoculation. Because of slow growth of Syn-
gonium, growth measurements were taken only for Gerbera and Nephrrolepis. 
The root system was washed of soil particles with running tap 
water, and above- and underground tissues were oven-dried sepa-
rately for 72 h at 65C before dry weight was recorded.

The analyses of chemical and physical characteristics as well as 
analysis of hydrophysical properties of substrates were conducted 
by the Centre de Recherche Premier (Rivière-du-Loup). Nutrient 
concentration in substrates was determined by saturation extrac-
tion methods (SEM) (Warnche, 1986). The following substrate 
physical and chemical characteristics were evaluated before culture: bulk density (BD), water content at saturation (WCS), grav-
itational water (macroporosity) (GW) (water tension <0.01 bars), 
available water (water tension = 0.1 to 0.1 bars) (AW), P-PO4, and 
pH (Table 1). Analyses confirmed that both fibric sphagnum 
peatmosses had lower bulk density and more macroporosity and 
available water than the fibric-mesic sphagnum peatmoss (sub-
strate 1). Of the two fibric sphagnum peatmosses (substrates 2 and 
3), substrate 3 had a higher GW and less available P. Substrate 1 
had a higher BD with the least GW and AW.

An analysis of variance was performed on SAS software (SAS 
Institute, 1982) using a general linear model on the mean of each 
experimental unit. The three species were analyzed separately. No 
transformation was conducted on percentage data since residuals 
were randomly and normally distributed. The variance of the 
different treatments was also homogeneous. For all characteristics 
studied, a Duncan multiple range test (P < 0.05) was used to 
identify differences among means.

Table 1. Analysis of physical and chemical characteristics of three peat-
based substrates (before culture).a

| Substrate | BD (kg·liter−1) | WCS (% v/v) | AW (% v/v) | GW (% v/v) | P-PO4 (ppm) | pH |
|-----------|----------------|-------------|------------|------------|-------------|----|
| 1         | 0.12           | 680         | 25.0       | 11.7       | 2.0         | 5.78|
| 2         | 0.05           | 1330        | 34.7       | 14.9       | 2.0         | 6.38|
| 3         | 0.06           | 1060        | 35.2       | 16.4       | 1.2         | 6.57|

P-PO4, water content at saturation (WCS), gravitational water (macroporosity) (GW) (water tension <0.01 bars), available water (water tension = 0.1 to 0.1 bars) (AW), P-PO4, and pH (Table 1). Analyses confirmed that both fibric sphagnum peatmosses had lower bulk density and more macroporosity and available water than the fibric-mesic sphagnum peatmoss (substrate 1). Of the two fibric sphagnum peatmosses (substrates 2 and 3), substrate 3 had a higher GW and less available P. Substrate 1 had a higher BD with the least GW and AW.

An analysis of variance was performed on SAS software (SAS Institute, 1982) using a general linear model on the mean of each experimental unit. The three species were analyzed separately. No transformation was conducted on percentage data since residuals were randomly and normally distributed. The variance of the different treatments was also homogeneous. For all characteristics studied, a Duncan multiple range test (P < 0.05) was used to identify differences among means.
Results

VAM fungal establishment and spread in micropropagated Gerbera, Nephrolepis, and Syngonium plantlets. VAM fungal establishment and spread were evaluated by measuring the intensity of root-length endomycorrhizae colonization (% REC). Extramatrical mycelium coming from infected root segments were observed on the root surface 4 weeks after Gerbera and Nephrolepis plantlets were transferred to mycorrhizal substrate (Fig. 1). Infection by VAM was observed after 8 weeks for Syngonium. The percentage of colonization increased rapidly from week 8 to week 16 for Gerbera and Nephrolepis, while it remained constant and slow for Syngonium. Differences in colonization intensity between G. intraradices and G. vesiculiferum became significant after 8 weeks for Nephrolepis, while significance was observed after 12 weeks for Gerbera and Syngonium.

Throughout the experiment, all tested species were infected more by G. vesiculiferum than by G. intraradices. Although no statistical comparison was conducted between the three species with respect to their receptivity to VAM infection, Gerbera was the most infected with 61% ± 2.3%, followed by Nephrolepis with 41% ± 2.8%, and Syngonium with 13.4% ± 3.6%. By the end of the experiment, G. vesiculiferum and G. intraradices had heavily infected the roots of Gerbera (67% and 55% REC, respectively) (Fig. 1A), moderately infected the roots of Nephrolepis (36% and 47%, respectively) (Fig. 1B), and weakly infected the roots of Syngonium (27% and 11%, respectively) (Fig. 1C).

Mycelium morphology within cortical cells also was dependent on the host plant. There was more arbuscule than vesicle development in Nephrolepis and more vesicle than arbuscule development in Gerbera. Only vesicles were apparent in Syngonium.

Effect of three PBS on symbiosis establishment. The different substrates had a strong influence on VAM symbiont establishment (Fig. 2). For the three species and the four sampling dates, there was no interaction between substrate type and VAM species. A higher colonization rate was obtained in the fibric PBS (substrates 2 and 3) than in the fibric-mesic PBS (substrate 1) at every sampling date for Nephrolepis and at 12 weeks for the others. A mycorrhizal infection was obtained after only 4 weeks in fibric PBS, while it was observed after 8 weeks within fibric-mesic PBS. In general, substrate 3 allowed for the best VAM colonization regardless of plant species.

Effects of VAM fungi and PBS on plantlet survival. The plantlet survival rate was determined after 4 and 8 weeks following transfer

Fig. 1. Colonization intensity of Gerbera (A), Nephrolepis (B), and Syngonium (C), with Glomus intraradices (O) and G. vesiculiferum (●) at 4, 8, 12, and 16 weeks after inoculation. Mean separation by t test (P ≤ 0.05).

Fig. 2. Effects of different peat-based substrates [substrate 1 (A), substrate 2 (■), substrate 3 (○)] on colonization intensity of Gerbera (A), Nephrolepis (B), and Syngonium (C) with Glomus intraradices at 4, 8, 12, and 16 weeks after inoculation. Mean separation by Duncan multiple range test (P ≤ 0.05).
from test tubes to artificial substrates. Both mycorrhizal inoculation and substrate influenced plantlet survival, and no interaction was observed between these factors. Differences in survival rates of Gerbera, Nephrolepis, and Syngonium plantlets inoculated and not inoculated with mycorrhizal fungi were not visible until 8 weeks after transplanting into inoculated media (Table 2). At this time, survival rates of inoculated plantlets were increased by 5.4% and 6.7%, with G. intraradices and G. vesiculiferum for Gerbera, and were increased by 4.6% and 5.7% with G. intraradices and G. vesiculiferum for Nephrolepis. The improved survival rate of mycorrhizal plants appears related to the extent of VAM colonization. There was no effect on Syngonium survival between VAM inoculated and noninoculated treatments.

Different substrates had a significant effect on the survival of the three species (Table 2). All three species planted in the fibric PBS (substrates 2 and 3) survived better than those planted in fibric-mesic PBS (substrate 1). Among the two fibric PBS, survival was higher in substrate 3 for both Gerbera and Nephrolepis. Substrate 3 had less available water, less available P, and was more aerated. Survival rate of plants in substrate 3 was significantly higher by 9.4% and 4.4% than in substrates 1 and 2 for Gerbera and also was significantly higher by 8.4% and 4.4% than in substrates 1 and 2 for Nephrolepis.

Effects of mycorrhizal PBS on plantlet growth and flower development. Shoot and root dry weights for both Gerbera and Nephrolepis were evaluated in response to mycorrhizal PBS. Both mycorrhizae and substrate treatments influenced growth of Gerbera and Nephrolepis plantlets, while there was no interaction between these factors after 4, 8, 12, or 16 weeks. The only exception was a significant interaction observed between VAM inoculate and substrate for Nephrolepis root dry weight after 16 weeks.

Shoot dry weights of Gerbera and Nephrolepis were increased significantly by VAM-inoculated treatments (Fig. 3). Gerbera inoculated with Glomus intraradices and G. vesiculiferum had, respectively, a 31.5% and 25.1% higher shoot dry weight than the control at week 16. The positive effect of VAM increased with the age of the plantlet and reached the highest absolute value at the end of the experiment.

The root growth of Gerbera and Nephrolepis also was influenced by mycorrhizae inoculation. VAM-inoculated plantlets had higher root dry weights than control plants, except at the first sampling period, where no increase in root dry weight was observed for Gerbera (Fig. 3a), and a slight reduction in root dry weight was observed for Nephrolepis (Fig. 3b). Type of PBS affected the growth effects recorded. In general, Gerbera and Nephrolepis grew significantly more in substrate 3 than in the other two substrates (Fig. 4). Indeed, shoot dry weight was significantly higher at all sampling dates for the two species with substrate 3 than with substrates 1 or 2. Moreover, for Nephrolepis plantlets, substrate 3 gave the highest root dry weight of any substrate used in this study (Fig. 4b). For Gerbera, differences in root dry weight between substrate 1 or 2 and substrate 3 was only observed at the end of the experiment (Fig. 4a).

Gerbera productivity was evaluated by the number of flowers, capitulum diameter, stem length, and stem diameter (Table 3). VAM-inoculated Gerbera plants produced larger and more flowers than noninoculated Gerbera. There were no differences be-

| Treatment | Gerbera Survival (%) | Nephrolepis Survival (%) | Syngonium Survival (%) |
|-----------|----------------------|--------------------------|-------------------------|
|           | 4 week | 8 week | 4 week | 8 week | 4 week | 8 week |
| Mycorrhizae |       |        |       |        |       |        |
| Glomus intraradices | 90.0  | 87.8 a* | 86.7  | 85.3 a | 92.6  | 90.0 a |
| G. vesiculiferum   | 92.7  | 88.9 a | 85.9  | 84.4 a | 94.1  | 92.2 a |
| None              | 92.2  | 83.3 b | 84.4  | 80.7 b | 93.3  | 91.9 a |
| Substrate |       |        |       |        |       |        |
| 1         | 90.0  | 82.6 c | 83.7  | 79.6 c | 90.0  | 87.8 b |
| 2         | 91.9  | 87.1 b | 84.4  | 82.6 b | 92.7  | 92.2 a |
| 3         | 93.3  | 90.4 a | 88.9  | 86.3 a | 93.3  | 91.9 a |

**Significance**

|               | Gerbera | Nephrolepis | Syngonium |
|---------------|---------|-------------|-----------|
| Mycorrhizae (M) | NS      | *           | NS        |
| Substrate (S)   | NS      | *           | *         |
| M x S          | NS      | NS          | NS        |

*Values within columns with the same letter are not significantly different (Duncan multiple range test, P < 0.05).

*NS: Non-significant or significant at P ≤ 0.05, respectively.
Discussion

This experiment has demonstrated that the VAM fungi *G. intraradices* and *G. vesiculiferum* can establish a symbiotic association with all three tested plant species. The percentage of root colonization for a given fungus varied among the different host plant species. This result confirmed the work of Mosse and Hayman (1973), who reported that plants of many species can be infected by VAM fungi, but the degree of VAM infection and its physiological effects can differ with different host-endophyte combinations. The difference in colonization intensity of VAM fungi might be attributed to the degree of plant receptivity, because the conditions of establishment were the same for the three species. The receptivity of different plant species to VAM fungi may result from the peculiar morphology of in vitro formed roots. Baylis (1972) proposed, in the “root hair hypothesis,” that plants are most likely to respond to VAM fungi if their root anatomy allows infection. This author showed that secondary roots and roots with root hairs are more sensitive to VAM infection than tap roots. The root hair hypothesis might well explain why colonization was slower for *Syngonium* than for the other two species, since *Syngonium* roots were thick and unbranched with few secondary roots and few root hairs, while in vitro-propagated *Gerbera* and *Nephrolepis* had well-developed root systems with abundant root hairs.

In our experiment, no significant differences in root colonization or growth were observed between *G. intraradices* and *G. vesiculiferum* at 4 weeks. When root colonization rate had increased =10% (Fig. 1), significant differences in growth could be observed (Fig. 3), thus suggesting that a relationship exists between root colonization and growth. Plants inoculated with *G. intraradices* had higher shoot and root dry weights than those inoculated with *G. vesiculiferum*, although *G. vesiculiferum* allowed a higher colonization rate than *G. intraradices* did. The results thus indicate that there is not always a strict relation between colonization rate and growth response of host plants. Mosse and Hayman (1973) reported that the most infective endophytes are not necessarily the most effective. VAM efficiency possibly is affected by differences in their symbiotic structures (e.g., arbuscules or vesicles), which could influence the nutrient exchange processes (Hayman, 1983).

The PBS composed of 75% peat and fertilized with a low level of available P did not inhibit mycorrhizal colonization. However, different types of the PBS, characterized on the basis of their porosity, significantly influenced symbiont establishment. The ideal substrate for mycorrhizal infection should provide an adequate and balanced water supply, and an abundant oxygen supply for capillary root growth. Comparing the three substrates used in this study, fibric PBS (substrates 2 and 3) was more aerated than the fibric-mesic PBS (substrate 1) (Table 1). Substrate 3, which had good aeration, more available water, and increased mycorrhizal fungi infection activity, stimulated shoot and root growth and improved plantlet survival. The lower colonization intensity for all species grown in substrate 1 can be explained by its high density and poor aeration. This substrate did not allow proper development of new secondary roots and root hairs normally associated with mycorrhizal fungi. Other studies also have shown that high aeration in a substrate is more suitable for root respiration and mycorrhizal fungus activity (Saif, 1981), and poor aeration may be a limiting factor for VAM fungus colonization and may result in low survival of plantlets (Ponton et al., 1990; Saif, 1981, 1984). Our results confirm these observations. Substrates having a fine texture, and normally used for seed germination, are not necessarily well suited for in vitro plantlet acclimatization and further growth in a greenhouse.

Normally, “acclimatization” lasts ≈4 weeks after transferring plantlets from test tubes to a greenhouse. However, VAM infection did not happen in the first 4 weeks following inoculation under our experimental conditions, despite the observation made by Piché and Peterson (1987) that infection, development, and penetration of hyphae and arbuscule and vesicle formation of *Glomus monosporum* took only 5 to 8 days for leek seedlings, and 8 to 15 days for cotton (*Gossypium hirsutum* L.), onion (*Allium cepa* L.), and pepper (*Capsicum annuum* L.) seedlings (Afek et al., 1990). Thus, VAM fungi apparently do not affect survival during acclimatization. This fact is most probably the result of delayed colonization and symbiosis, which had not yet formed at week 4.

The lag phase of mycorrhizal colonization probably can be attributed to two main causes. First, root morphology and anatomy of tissue-cultured plants are different from that of seedlings (Pierik, 1987) and probably not amenable to colonization by VAM. Colonization can occur only when new roots are initiated. Second, culture conditions maintained during acclimatization may be unfavorable to VAM colonization. It is well recognized that micropropagated plantlets should be maintained in soil near moisture saturation for the first 2 to 4 weeks after transfer from test tubes.
to soil. Under water saturation, soil \( O_{\text{2}} \) diffusion is limited. Low \( O_{\text{2}} \) concentration can severely inhibit VAM spore germination and root colonization (Saif, 1981), which may explain why substrate 1 (denser and with less macroporosity than the others) was also the substrate with the lowest percentage of root colonization. Moreover, Reid (1978) reported that moisture saturation in soil reduced VAM colonization by 50%. Our results reveal that to have a positive effect from VAM inoculation during acclimatization, substrate moisture conditions must be controlled precisely.

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