

reason we take every step to push our seedlings to maximum size in a single growing season

Good seedling production practices must continue until the crop is harvested, graded, stored and shipped making certain a minimum amount of stress is placed on the plant material. Great care is exercised to apply a protective spray in the field as soon as the seedlings are dug and placed in pallets. The pallets are tarped for additional protection while transported to the storage buildings. They are held in high humidity storage (98 to 100% relative humidity) during the storage period, which begins in November and extends through the following May for a portion of the crop. When grown properly and handled carefully, one can approach a near perfect stand when the seedlings are transplanted to the nursery for future production.

**SIGNIFICANT ENVIRONMENTAL AND BIOCHEMICAL
FACTORS IN SEED GERMINATION OF *LIRIOPE MUSCARI*
AND TWO RELATED TAXA**

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Liriope muscari (Decne.) Bailey, big blue liriope, is one of the most commercially important groundcovers in the southeastern landscape, and is also widely used in the southwest and California. Hardy to Zone 6, it could be used in additional geographic areas. The 1 to 2 foot grass-like evergreen foliage; lilac-purple flowers borne on a spike above the foliage; sun and shade tolerance; and adaptability to a wide range of soil types are traits contributing to its popularity. *Liriope* displays a high degree of salt tolerance which makes it particularly useful in coastal landscapes (5,20).

Abundant blue-black, single-seeded berries are produced on upright spikes in the fall. Seeds are globose and the embryo is surrounded by copious, hard endosperm. A deep blue-black skin envelopes a purple, pulpy inner matrix (collectively called pulp). Seed appears to be a logical method of propagation, although division, which is not only time consuming but expensive, is the only method referred to in the literature (1,5,20).

Dormancy mechanisms in other members of the Liliaceae, specifically *Trillium grandiflorum* (Michx.) Salisb. (3), *Polygonatum biflorum* (Walt) Ell. (3) and *Lilium* (2) species posed ques-

tions as to the germination requirement of *Liriope muscari*. The subsequent studies were designed to determine the endogenous and/or exogenous factors that are necessary for seed germination in *Liriope muscari*. It was hoped that a commercially feasible recommendation for seed propagation could be established.

Additionally, similar fruit morphology and paucity of information pertaining to their seed germination prompted germination studies of two related taxa. The taxa included: 1) *Liriope muscari* L. 'Variegata', variegated liriope, similar to *L. muscari* in morphological and cultural requirements, with the exception of leaves having two white marginal stripes and a central green band, and 2) *Ophiopogon japonicus* (Thunb) Ker., mondo grass, a member of a closely allied liliaceous genus. *Ophiopogon* resembles liriope in gross morphology, differing mainly in its shorter height (16 to 37 cm), narrower leaves (0.2 cm), reduced cold hardiness (Zones 8 to 10), and a flower scape that does not exceed the height of the foliage. These two grasslike perennials are also valuable groundcovers in the southeast, and are commonly propagated by division, with no documentation of the specifics of seed propagation present in the literature (1,5,9)

The work is divided into three parts: 1. determining the effects of stratification, depulping, and growth regulators on *Liriope muscari* seed germination, 2. seed germination of *Liriope muscari* 'Variegata' and *Ophiopogon japonicus*, based on the most successful methods with *Liriope muscari*, and 3. characterization of substances inhibitory to seed germination in the fruit pulp of *Liriope muscari*

1. Fruit of *Liriope muscari* was collected on November 3, 1979 at the University of Georgia Botanical Garden, Athens, and stored dry for 120 days at 5°C. Intact fruits were: (a.) soaked for 24 hr in distilled water, placed in a 0.5% sodium hypochlorite solution for 15 min, rinsed in distilled-deionized water; or (b.) given only the 0.5% sodium hypochlorite sterilization treatment. Both groups were then placed in polyethylene bags with moist sphagnum peat and held at 21°C in a Precision Scientific incubator. For each treatment 150 seeds were used.

Depulped seeds were either soaked for 24 hr in water (control), or the following growth regulators: gibberellic acid (GA_3), 30, 60, 90 ppm; kinetin, 30, 60, 90 ppm, and GA_3 + kinetin, 30:60, 45:45, 60:30 ppm. The seeds were then rinsed, treated with sodium hypochlorite, rinsed with distilled-deionized H_2O and placed in polyethylene bags with moist sphagnum peat at 21°C. All treatments for intact and depulped seeds were duplicated and placed in cold stratification at 5°C to

determine whether the species needs a chilling requirement prior to germination. When a majority of the seeds germinated (after 6 weeks) in warm stratification, evaluations were made of percent germination, radicle length, and presence of shoots. The experiment was conducted in a completely randomized design with 13 treatments. All treatments were replicated 6 times with 10 seeds per replicate. Analyses of variance and chi-square tests were performed according to Ott (13).

Radicle emergence from depulped seeds was evident after 3 weeks. At the end of the 6th week in warm stratification, radicle emergence in excess of 90% and shoot emergence ranging from 68-88% were observed in the depulped treatments (Table 1). Germination percentages for both radicle and shoot emergence among all depulped treatments were not significantly different. However, seeds soaked in water had shorter radicles and less shoot development compared to those receiving growth regulator treatments. Among the various growth regulator treatments, GA₃ at the various concentrations produced longer roots with secondary branching and shoots in excess of 40mm. GA₃ + kinetin treatments produced roots of similar size to GA₃ alone but shoot development was noticeably less. Kinetin produced shoots and radicles intermediate between GA₃ and GA₃ + kinetin.

Table 1. Effect of stratification, depulping, and growth regulator pretreatments on the germination of *Liriope muscari* seed

Treatment	Conc (ppm)	Germination (percent)	
		Radicle emergence	Shoot emergence
<i>Depulped</i>			
Cold stratification		0 a ^z	0 a
Warm stratification		90 b	68 b
GA ₃	30	100 b	88 b
	60	95 b	83 b
	90	97 b	88 b
Kinetin	30	92 b	75 b
	60	95 b	80 b
	90	93 b	77 b
GA ₃ + kinetin	45 + 45	87 b	70 b
	30 + 60	98 b	87 b
	60 + 30	97 b	88 b
<i>Intact</i>			
Warm stratification			
Water soak		38 c	23 c
Non-soak		25 d	7 d

^z Mean separation within columns by X² test, 5% level

In contrast, intact fruits showed limited germination and, after 6 weeks, soaked and non-soaked seeds germinated (radicle emergence) 38 and 25%, respectively. Shoot emergence was

also reduced, being 23 and 7% for soaked and non-soaked, respectively.

2. Fruits of *Liriope muscari* 'Variegata' and *Ophiopogon japonicus* were collected from plantings on the University of Georgia campus, Athens, in early December, 1980. Fruits were mechanically depulped by placing them with an equal volume of distilled-deionized water in a blender (blades masked), dusted with Captan® 50% WP (replacing the sodium hypochlorite treatment) and placed in polyethylene bags for warm stratification (3). Depulping was compared to the control treatment in which fruits were left intact. Both treatments for each taxa were warm stratified in a Precision Scientific lighted incubator ($18\mu\text{Em}^{-2}\text{sec}^{-1}$, 24°C). Each treatment was replicated five times, with 60 seeds per replicate. The experimental design was completely randomized. After 6 weeks in warm stratification, seeds were evaluated for germination. Radicle and shoot emergence were used as the germination indices. Seedlings were then transplanted and grown under greenhouse conditions (13°C night, 24°C day). Differences in germination percentages between depulped and intact treatments were statistically analyzed by a t-test according to Ott (13). Seedlings of variegated liriope were evaluated as to type of leaf variegation pattern after 6 weeks in the greenhouse.

Germination percentages for depulped seeds and intact fruit of *Liriope muscari* 'Variegata' and *Ophiopogon japonicus* are shown in Table 2. In both taxa, depulped seeds germinated at higher percentages than controls. Radical emergence percentages were 77 and 74% for variegated liriope and mondo grass seeds respectively. Intact fruits of both taxa showed negligible shoot emergence (3%) after 6 weeks in stratification. Seeds continued to germinate sporadically in the greenhouse.

Table 2. The effect of depulping on germination of *Liriope muscari* 'Variegata' and *Ophiopogon japonicus* seed

Taxa	Treatment	Percent germination ^z	
		Radicle emergence ^y	Shoot emergence
<i>Liriope muscari</i> 'Variegata'	Intact (control)	25% a ^x	3% a
	Depulped	77 b	33 b
<i>Ophiopogon japonicus</i>	Intact	28 a	3 a
	Depulped	74 b	54 b

^z Mean of five replications

^x Mean separation between treatments by t-test, 5% level

^y After six weeks warm stratification

Sixty-five percent of *L. muscari* 'Variegata' seedlings exhibited some form of variegation: 49% of these seedlings had the typical white-margined variegation pattern, 9% contained

several heterogenous stripes, and 7% were half white/half green (Table 3) Of the remaining seedlings, 20% were achlorophyllous (albino), and 15% were either solid yellow or green. Generally, albino seedlings did not survive more than 2 weeks under greenhouse conditions

Table 3. Variegation patterns and their percent distribution in seedlings of *Liriope muscari* 'Variegata'

Variegation pattern	Percent
White marginal stripes	49% ^{z y}
Several heterogeneous stripes	9
Half green/half white	7
Albino	20
Not variegated	15

^z Total seedlings observed = 141

^y Observed after six weeks under greenhouse conditions (12 weeks past sowing)

3 The aforementioned work with seed of *Liriope muscari* showed that removal of the pulp significantly enhanced germination. Water extractions of the pulp applied to cucumber seeds indicated the presence of a water soluble inhibitor. These water extracts take on the intense blue-black color of the fruit skin and pulpy matrix (collectively termed the pulp) at a neutral pH. No information as to which compound(s) impart the distinctive deep blue color or the inhibitory properties is available for this species.

Germination inhibitors are mostly non-specific, i.e., one inhibitor will prevent germination of seeds of several species, the sensitivity of various species varying with concentrations applied. A bioassay is a common procedure for determining the presence of germination inhibitors in plant tissue. Test seeds are allowed to imbibe the plant juice/sap or a partially purified plant extract directly (9,12,17). Any high quality seed that will germinate 90 to 100% can be used as the test material. It should be noted that the bioassay is a crude indication of the presence or absence of an inhibitor and tells nothing of either their chemical nature or mode of action. Individual components of the plant extract need to be isolated and identified prior to use in a bioassay and before any specific inhibitor can be named.

The following lines of evidence suggested that the fruit pulp should be examined for phenolic compounds (including anthocyanins) as a prerequisite for characterizing its inhibitory nature: (a.) the crude pulp solution was blue at pH 5-6, red at pH 4; (b.) the inhibitor was present in water extracts, and thus is apparently water soluble; (c.) boiling of the extract did not decrease inhibition, which suggests the inhibitor is not a pro-

tein, whereas, anthocyanic inhibitors retain their activity after boiling (11); (d.) the addition of polyvinylpyrrolidone (Poly-ClearAT^R), a phenol-complexing agent caused partial decrease of inhibition in cucumber bioassays; and (e) a paper-chromatographic survey revealed high concentrations of anthocyanins and phenolic acids.

Liriope muscari fruit was collected in January, 1981, on the University of Georgia campus, Athens. Pulp was mechanically removed as previously described, air dried for 48 hr and finely ground in a Wiley mill. Dried pulp was extracted in distilled/deionized water for three 12 hr rinses. The rinses were combined and taken to dryness *in vacuo*. Eighty mg of dried crude extract was dissolved in 10% MeOH/H₂O and applied to a 40 × 8 cm Sephadex R(25-100 μ m) column for bulk isolation of component fractions in *liriope* pulp. The individual fractions would be applied to a bioassay to test for germination inhibition.

A graded series of increasing percentages of neutral MeOH in water (10% MeOH, 20% . . . 100%) served as the column chromatography solvent. UV/visible bands were collected as fractions, evaporated to dryness and weighed. The resulting fractions were monitored using 2D paper chromatography (PC) to determine the presence of anthocyanins, other flavonoids, and phenolic acids in each. The solvent in the first dimension was *tertiary*-butanol/acetic acid/water, 3:1:1 (TBA); and acetic acid/water, 15:85 (HOAC) in the second dimension. Each fraction was also subjected to UV/visible spectrophotometry on a Beckman DBG spectrophotometer. R_f values, color reactions and spectral data were used to identify PC spots as to phenolic class. Further purification of the fractions was not attempted. Each pre-weighed crude fraction was dissolved in 10 ml of water or MeOH, depending on its solubility (fractions that came off the column first were readily soluble in water, whereas later fractions were more soluble in MeOH). Since the number of seeds and quantity of pulp used to make the crude water extract was known, uniform dilution of each column fraction gave concentrations approximating that found in one *Liriope* fruit. Water soluble fractions were applied directly in 2 ml aliquots to a cucumber seed bioassay consisting of 10 *Cucumis sativus* 'Poinsett' (Poinsett cucumber) seeds placed on a double layer of pre-moistened Whatman #2 filter paper in a petri dish. The dishes were covered and placed in a 24°C lighted Precision Scientific incubator. Each fraction was applied to three replicate petri dishes. For water insoluble fractions (dissolved in MeOH), 30 cucumber seeds were tied in a single layer of cheesecloth and suspended in the alcoholic solutions for 30 seconds. The seed bundles were then suspend-

ed in air to completely dry (methanol evaporated), leaving a relatively uniform coating of the dissolved fraction on each seed. The seeds were then divided into three replications of 10 cucumber seeds each and treated identically to the water fractions. Water and plain MeOH were used as controls for each of the above procedures. After four days in incubation, germination percentages in terms of radicle and shoot emergence were obtained

Fractions affecting the greatest inhibition were combined to determine whether some synergism between several substances contributed to a greater degree of inhibition, as would be evidenced in an intact fruit. Pair wise and collective combinations were made (1 ml. 1 ml, v/v) and applied to three replicate petri dishes each. These were also incubated for 4 days at 24°C and evaluated for extent of inhibition.

— Significant differences in mean germination percentages among the fraction treatments were determined by means of Duncan's multiple range test.

To tentatively identify the phenolic acids present, several known standards were chromatographed in TBA and HOAC and their R_f values and color reactions compared to phenolic acid-like spots appearing in the individual fraction chromatograms.

Nine distinct bands from *Liriope muscari* pulp were eluted as crude fractions from the Sephadex® column by a graded series of neutral MeOH solvents. Germination percentages resulting from the application of each fraction to a cucumber seed bioassay are shown in Table 4. A decrease in radicle and shoot emergence, and in general radicle length, was observed in all of the pulp-fraction treatments as compared to the controls. However, radicle emergence was significantly reduced by five fractions and shoot emergence by seven (Table 5). When considering radicle and shoot emergence together, fractions 1, 5, and 7 gave the most pronounced inhibition. Percent radicle emergence for these three fractions was 50, 46.7, and 53.3% respectively, in contrast to 85% in control treatments. Shoot emergence was more markedly affected; fractions 1, 5, and 7 averaging 18% shoot emergence while controls had 60%. Fractions 3 and 4 were not inhibitory to radicle emergence, but did significantly inhibit shoot development.

The effects of three combination treatments are seen in Table 6. When fractions 1 and 2 were combined, higher germination percentages resulted than when either were applied alone. Chromatographically, both 1 and 2 contained the same compounds, those in 2 being less concentrated. Therefore, it is believed that the higher germination seen is a dilution effect,

Table 4. The effect of nine *Liriope muscari* pulp fractions on the germination of 'Poinsett' cucumber seeds

Fraction	Mean ^z percent				Mean Radicle length
	Radicle emergence		Shoot emergence		
H ₂ O control	87	a ^y	60	a	3.8 cm
MeOH control	83	a	59	a	2.9
1	50	b	17	b	0.9
2	53	b	27	b	0.8
3	64	a	27	b	2.2
4	67	a	30	b	2.2
5	46	b	17	b	2.0
6	67	a	50	a	2.9
7	53	b	20	b	2.4
8	67	a	40	a	3.3
9	60	b	30	b	3.0

^z Mean over three replications

^z Mean separation within columns by Duncan's multiple range test, 5% level

Table 5. Significant inhibition of 'Poinsett' cucumber seed germination among *Liriope muscari* pulp fractions

Fraction	Significant inhibition	
	Radicle emergence	Shoot emergence
1	●● ^z	●●
2	●	●
3		●
4		●
5	●●	●●
6		
7	●●	●●
8		
9	●	●

^z ● = significant inhibition, ●● = excessive inhibition

the toxicity of compounds being found in 1 and 2 being diluted in half as a consequence of this combination. Fraction 2 was not included in the collective fraction combination (1 + 5 + 7) due to this apparent dilution affect with 1. Radicle emergence in seeds treated with fraction 5 + 7 was low, with percentages similar to those seen in each singularly. In addition, shoot emergence was notably lacking in this combination. This suggests that different, independently toxic compounds are present in these two fractions, which upon combination, have an additive effect that exceeds a dilution effect, to express significant inhibition. When fractions 1, 5, and 7 were combined, the inhibition appeared to be synergistic. Radicle emergence was reduced to 20% and no shoots developed. The effects of fractions 1, 5, and 7 in combination suppressed germination to below levels seen in any of the three fractions applied alone

Table 6. The effect of three pulp fraction combinations on the germination of 'Poinsett' cucumber seeds

Fractions	Mean ^z percent		Mean Radicle length (cm)
	Radicle emergence	Shoot emergence	
1 + 2	70 a ^y	23 a	1.0
5 + 7	57 b	0 b	0.4
1 + 5 + 7	20 c	0 b	0.1

^z Mean over three replications

^y Mean separation within columns by Duncan's multiple range test, 5% level

Based on chromatographic data (Rf values and color reactions), the relative composition of each fraction is seen in Table 7. Classes of compounds identifiable among the various fractions are: anthocyanins, phenolic acids, anthoxanthins, and a spot that suggests a polyphenol such as a tannin. It is evident that more than one of each type of compound is present in *Liriope* pulp. Fractions 2 and 6 contain different anthocyanins; at least four different anthoxanthins are seen between fractions 6, 7, and 8; and not less than five unique phenolic acid spots are found between fractions 5 and 7. Fractions 5 and 7, in addition to anthocyanins and anthoxanthins, contain the highest preponderance of phenolic acids. Fractions 2, 3 and more so 1 and 5 contain the tannin-like substance. Spectral data substantiated these findings and indicated that the anthocyanins were of the delphinidin type.

Comparison of Rf values and color reactions of known phenolic acids on paper chromatograms (also run in TBA and HOAC) led to the tentative identification of pyrogallol and caffeic acid as phenolic acids present in fraction 1 and 1 and 7, respectively.

Table 7. Presence of various phenolic compounds within each *Liriope muscari* pulp fraction

Fraction	Anthocyanins	Phenolic Acids	Anthoxanthins	Polyphenol (tannin)
1	X ^z			X
2	X			X
3			X	X
4			XXX	
5	X	XXX		X
6	X		XX	
7	X	XX	XX	
8			XXXX	
9			X	

^z X = presence of compounds, multiple X's for each distinct number evidenced

Removal of the pulp significantly enhanced the percentage and rate of germination of *Liriope muscari*. This suggested that

one or more inhibitors may be present in the pulp (pericarp wall) Since water soaking of intact seeds resulted in higher germination percentages (38%) than non-soaked (25%), it appeared that the inhibitor(s) might be water soluble.

It should be noted that seeds of all treatments placed in cold stratification (5°C) showed no germination after 6 weeks. These seeds did germinate when sown in flats and maintained at 21°C. The germination percentages were similar to the warm stratified seeds. This indicated a moist, cold period is not a prerequisite for *Liriope muscari* seed germination.

Regulation of seed dormancy in *Liriope muscari* does not appear to be as complex as *Trillium*, *Polygonatum*, and other liliaceous species (2,3,4,18). If the pericarp wall is removed, uniform germination will occur after 6 weeks in warm stratification (21°C) or a similar environment.

Successful germination of variegated *liriope* and mondo grass seed indicates that their germination requirements are indeed similar to those of *Liriope muscari*. Although germination percentages did not reach the 90% of *L. muscari* in six weeks, they were sufficiently high that the authors feel seed propagation should be considered a feasible method of commercial production for all three taxa. Variegated *liriope* seed produces seedlings with heterogenous leaf variegation patterns, but if properly identified as such, might readily be marketed in the trade when production time and cost are factors. Variegation patterns of established vegetatively propagated *liriope* plantings on the University of Georgia campus were examined. It was evident that some plant to plant and even within-plant variation in leaf variegation patterns does exist, going undetected in the overall appearance of a large planting. A reliable method of seed propagation permits breeding and selection for superior types.

The similarity in response of *Ophiopogon japonicus* to *Liriope muscari* is not surprising, since they are so clearly associated morphologically as to have been considered members of the same genus (1,19). The genera have been confused in the trade, and much of what is grown as *Ophiopogon japonicus* 'Variegatus' is actually *Liriope muscari* 'Variegata' (20). *Ophiopogon* bears 3 to 6 viable fruits per spike on a mature plant, compared to the 15 to 30 of *Liriope* species observed, but in view of its inherently slower rate of stoloniferous multiplication, seed propagation would seem as economical or more so than the division methods commonly practiced.

Several classes of phenolic compounds are present in *liriope* pulp. flavonoids (anthocyanins and anthoxanthins), phenolic acids and a tannin-like polyphenol. It appears that certain classes of these phenolic compounds (especially phenolic

acids and tannin-types) when present in the individual pulp fractions, impart a greater degree of toxicity toward seed germination (Table 7). The greatest germination inhibition is seen in those fractions containing both anthocyanins and phenolic acids or the tannin-like substance. Fractions containing only anthocyanins are less toxic than those with phenolic acids or tannins, but more toxic than those containing anthoxanthins alone (anthoxanthins being non-charged flavonoid compounds). It appears that no one phenolic compound is solely responsible for the inhibition of seed germination by *Liriope* pulp, but rather synergistic, or at least collective effects, of several potent phenolics. Indeed, caffeic acid, found in two of the most toxic pulp fractions, has been isolated as a primary germination inhibitor from tomato juice (6,8,11). Anthocyanins and tannins are also well known for their potent inhibition in several biological systems (10,11,15,16)

The mode of action for the particular phenolic inhibition cannot be determined from our study, but the participation of phenolics is not surprising as nearly all naturally occurring phenolic compounds possess some biological or pharmacological activity. This propensity is related to the phenolic $-OH$ group's strong affinity for proteins and therefore enzymes (11). Phenolic interference may take the form of disruption of enzyme activation, from which the enzyme-dependent (e.g. α -amylase, proteinase) seed germination processes are not immune. Several investigators have noted the interaction between phenolic compounds and various growth regulators, some strongly allied to seed germination (gibberellic acid, cytokinins) (8,11). Of interest in the results of this experiment is the fact that shoot emergence was more severely inhibited than radicle emergence, implying a separation in the physiological controls of these two processes.

The presence of water soluble inhibitors in the fruit pulp of *Liriope muscari* may have ecological significance. Endogenous inhibitors have been known to prevent germination in unsuitable environmental conditions and act in successional preference (14). Since *Liriope* fruits mature in the late fall, presence of an inhibitor might insure seedling emergence in spring, when climatic conditions are more amenable to survival. Also possible are exogenous allelopathic or phytoalexin-like properties that may affect the surrounding microenvironment as these phenolic compounds are released during pulp degradation in the soil (24)

While limited by time constraints, these data provide *prima facie* evidence for the endotoxic effects of phenolic compounds on the germination of *Liriope* seeds. Ultimate refinement would, of course, require isolation and identification

of each of the individual phenolics to provide specific knowledge of their contribution to the toxicity.

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