naturally, thus saving energy. An interesting aspect of our April cuttings was that some cultivars that had low rooting percentages in May/June did very well while some cultivars that we never had trouble with did poorly in April.

All the azalea cuttings are potted since we are selling liners and it is easy to handle them this way, and we are planting by a machine. The machine consists of two Holland Peat Pot Planters, mounted offset on a tool bar. The boys drop the peat pots into the guides which are then picked up by the fingers of the machine and dropped into a furrow made by the shoes. Rows 1 and 3 are planted, then the tractor comes back over the bed and plants rows 2 and 4. The plants are then mulched and left for 2 seasons at which time we get a heavy 12" to 15" plant.

INTERNAL FLOODING OF RHODODENDRON LEAVES IN WINTER STORAGE¹

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Abstract. Internal leaf flooding is caused by movement of excessive water into leaves by root pressure while transpiration is inhibited by high relative humidity. Experimental evidence indicated that neither the flooded condition, nor freezing alone cause leaf injury. Flooded leaves were somewhat less cold hardy than normal leaves. Holding at low temperatures for 20 hours or more caused much more injury to both normal and flooded leaves than freezing for 2 hours. Tests of leaves sampled in Febuary revealed a wide variation in cold hardiness among cultivars and among plants of the same cultivar in the field and in storage. Suggestions are given for clearing leaves of internal flooding and for preventing injury associated with flooding.

One of the major reasons for placing plants in winter storage is for protection from damage. Nurserymen are concerned when storage injury develops and demand an explanation and recommendations for avoiding it. Questions have arisen about a condition called internal leaf flooding that may occur on rhododendron in storage.

Normal leaves have air-filled intercellular spaces occupying perhaps 10 to 20% of the leaf. Flooded leaves have dark blotches due to water infiltration of the intercellular spaces. It is not surprising that the discovery of this condition on

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rhododendron in storage causes concern, because it is not seen in the field and it can be an indication of leaf injury. Our observations indicate that leaf flooding occurs rather commonly on certain cultivars in storage without being associated with any injury at all. In fact we believe that the condition may develop and disappear without being seen by the nurseryman.

CAUSE OF LEAF FLOODING

Internal leaf flooding is caused by a combination of two conditions: (a) practically 100% relative humidity and probably wet leaves, which prevent any loss of internal water from the leaves, and (b) water being forced into the leaves under pressure.

Winter storages for rhododendron are usually designed to provide high relative humidity, using polyethylene as a vapor barrier, in order to prevent leaf damage from desiccation, especially while root balls are frozen. Very high moisture conditions develop in these storages during periods of rainy weather. However, the process by which water is forced into the leaves is not as apparent. Under conditions of low transpiration, roots of plants may accumulate nutrient salts in the xylem to the point that the osmotic concentration in the root xylem is considerably higher than in the soil water. Water then moves into the root xylem by osmosis, developing a pressure approximately equal to the difference in the osmotic concentrations inside and outside the root. Since the xylem is more or less a continuous open system from roots to leaves, the pressure in the roots forces water up the stem and into the leaves. This "root pressure" has been measured to reach as high as 2 atmospheres, or about 29 p.s.i. Root pressure accounts for exudation of water droplets at night from some foliage plants and for "breeding" of grape vines and birches when cut in the spring before leaf expansion. Further information on root pressure in plants can be found in Kramer (1).

Some nurserymen believe that leaf flooding is associated with below-freezing temperatures. It seems certain that root pressure could not force water into the leaves while the soil is frozen, because ice could not move from the soil into the root, or up the stem to the leaf. Furthermore, it is unlikely that nutrient salts would be accumulated in the roots while soil and roots are frozen. It is possible that freezing and thawing could somehow stimulate the salt accumulation process, but to our knowledge this has not been investigated.

We have been asked whether a heavily fertilized rhododendron is more likely to develop leaf flooding than a lightly fertilized plant. There are reports in the literature (2) that high nitrogen fertilization increases root pressure in some plants, so by inference it might increase leaf flooding.

Leaf flooding does not occur in the field because transpirational loss of water from leaves prevents the "back-up" conditions required for flooding. Transpiration also keeps water moving through the xylem, sweeping salts out so that the concentration is too low for osmotic pressure to develop.

In summary, the sequence of events leading to internal leaf flooding in storage is (a) an extended period of high humidity while the soil ball is not frozen; (b) followed by a period of extremely high humidity and probably wet leaves; (c) salts accumulate in root xylem; (d) osmotic pressure forces water into the root xylem, through the stem to leaf cells and (e) when the leaf cells become fully turgid, root pressure forces water into spaces between cells that are normally filled with air.

INJURY FROM INTERNAL FLOODING

We have seen many cases of leaf flooding in storage without any resulting damage. The flooding disappears and leaves become normal in a few hours or days when the weather changes from rainy to dry and sunny so that water can evaporate from the leaves. Nurserymen have reported, however, that severe injury does occur, especially if the leaves freeze while flooded. Therefore, research was conducted to determine if flooded leaves were more sensitive to injury than normal leaves.

Three Rhododendron cultivars were studies: 'Nova Zembla', said to be the most frequently flooded, 'Mrs. P. den Ouden', also frequently flooded, and 'Roseum Elegans', never known to show flooding. Flooding was produced experimentally in leaves on 6 to 8-inch stems. The leaves were enclosed in a polyethylene bag and water forced in the cut end of the stem under 30 to 50 p.s.i. pressure. For freezing tests, leaves were removed and frozen at 5°F/hr in plastic tubes in a temperature-controlled liquid bath. They were thawed slowly and examined visually for injury after a few days at room temperature. Typically, the first indication of injury was browning of midribs and veins (rated as slight injury); lower temperatures produced black or brown areas. Browning or blackening of 75% of the leaf was rated as severe injury. Four to six leaves provided experimental replications.

In artificially flooding the leaves it was observed that 'Roseum Elegans' required more time at a given pressure than the other two cultivars (Table 1). This may have been due to slower movement of water through the stem caused by either smaller xylem tubes, or more obstacles, or both. The greater re-

sistance to water movement in the stem of 'Roseum Elegans' could account for the fact that leaf flooding is rarely seen in this cultivar, although it could occur if conditions for flooding persisted long enough.

Table 1. Time required to flood leaves of three rhododendron cultivars by forcing water through cut end of stems.

	——————————————————————————————————————
30 p.s.i.	50 p.s.i.
10-15 min	5-10 min
15-20	10-15
45	25-30
•	10-15 min 15-20

Six branches of each cultivar with flooded leaves were enclosed in polyethylene bags, with cut ends in water, and placed in dark storage just above freezing. After 6 weeks, the branches with still flooded leaves were removed from storage and exposed to room temperature. The flooding disappeared within 24 hours and no injury could be seen. These results confirm that internal leaf flooding alone is not especially harmful.

Since freezing has been suggested as a cause of injury to flooded leaves, tests were conducted on the relative cold hardiness of flooded and normal leaves. In the first tests, leaves were held frozen for 2 hours at test temperatures from 20° to -30°F (Table 2). Normal leaves of 'Nova Zembla' and 'Roseum Elegans' collected from the field were not injured. Flooded leaves were slightly to moderately injured by the lowest temperatures. Normal and flooded leaves of 'Mrs. P. den Ouden' from the storage were about equally injured by 10°F and lower temperatures. These results show that freezing alone does not necessarily damage flooded leaves, since flooded 'Nova Zembla' leaves were frozen at -10°F without injury. Likewise flooded 'Roseum Elegans' leaves were frozen at 0°F and 'Mrs. P. den Ouden' leaves were frozen to 20°F without injury. The results do suggest that flooded leaves are more sensitive than normal leaves to freezing injury. Apparently, however, the cold hardiness of flooded leaves is related to the cold hardiness of normal leaves of the same plant; i.e., when normal leaves are very hardy, flooded leaves are also quite hardy.

Table 2. Injury to rhododendron leaves from 2 hours at several freezing temperatures (°F).

Cultivar & Source	Condition	20°	10°	0°	-10°	-20°	-30°
'Nova Zembla'	Normal	01	0	0	0	0	0
(field)	Flooded	0	0	0	0	+	+
'Roseum Elegans'	Normal	0	0	0	. 0	0	0
(field)	Flooded	0	0	0	+	++	++
'Mrs. P. den Ouden'	Normal	0	++	+++	+++	++++	+++
(dark barn storage)	Flooded	0	+++	+++	+++	$+ \div +$	+++

¹ Injury sumbols: 0 no injury, + slight injury, ++ moderate injury, +++ severe injury.

Since leaves in storage may be frozen for several hours, a test was conducted in which normal and flooded leaves of the two hardier cultivars were held for 20 hours at three test temperatures; 0°, -10° and -20°F. The procedure used was such that leaves exposed to the two lower temperatures were also exposed to the higher temperatures, so that those held 20 hours at -10°F had also been held 20 hours at 0°F, and those held 20 hours at -20°F had been held 20 hours at both 0°F and -10°F. These long periods of freezing caused much more injury to leaves of the two hardy cultivars (Table 3), especially at -10°F and -20°F, than when the freezing time was only two hours (Table 2). Flooded leaves showed slight to moderate injury after 20 hours at 0°F, whereas normal leaves were uninjured (Table 3). Generally the differences in hardiness were not of great magnitude. In another test (data not shown) leaves were held frozen at 20°F for 9 days. Flooded leaves of 'Mrs. P. den Ouden' from dark storage were severely injured, but normal leaves were not injured. Leaves of 'Nova Zembla' from a poly house were uninjured, whether flooded or not.

Table 3. Injury to rhododendron leaves from being held 20 hours at 3 freezing temperatures (°F)¹.

				
Cultivar	Condition	0°	-10°	-20°
'Nova Zembla'	Normal	0^{2}	+++	+++
(field)	Flooded	++	+++	+++
'Roseum Elegans'	Normal	0	+	+++
(field)	Flooded	+	++	+++

Leaves exposed to -10°F were first exposed to 20 hours at 0°F; similarly, leaves exposed to -20°F were exposed to 20 hours at each of the 2 higher temperatures.

The results of our freezing tests show that flooded leaves are less cold hardy than normal leaves, but they do not allow us to give a precise degree difference. Apparently the difference may vary with cultivar and with the hardiness of the normal leaves. A difference of about 10°F could be useful, although admittedly inaccurate, rule of thumb.

A previous test (Table 2) had compared leaf hardiness of two cultivars in the field and one cultivar from storage, the latter being much less hardy than those from the field. Since internal leaf flooding is a storage condition, it seemed desirable to compare the leaf hardiness of cultivars in storage. With the kind of permission of Weston Nurseries, we were able to collect samples of several cultivars from storage and field in February. The results of hardiness tests of three cultivars are shown in Table 4. A particularly interesting comparison for 'Nova Zembla' revealed that plants stored in the relatively warm barn (min

² Injury symbols: 0 no injury, + slight injury, ++ moderate injury, +++ severe injury.

25°F) were less hardy than plants in the unheated poly house (min 10°F), and both were less hardy than plants in the field. Both 'Dr. H.C. Dresselhuys' and 'Mrs. P. den Ouden' were 15 to 20°F less hardy in barn storage than in the field, and 'Mrs. P. den Ouden' was markedly less hardy than either of the other cultivars. Since flooded leaves are perhaps 10°F less hardy than normal leaves, we might expect injury to flooded leaves in these dark storage if the storage air temperature were to fall briefly to 0°F for 'Nova Zembla', 10°F for 'Dr. H.C. Dresselhuys' and 20°F for 'Mrs. P. den Ouden'. Injury might occur at even higher temperatures if the cold lasted for several days.

Table 4. Hardiness of rhododendron leaves (not flooded) collected in February from field and storage.

Cultivar	Source	Estimated min. temp. (°F)	Date Collected	Damaging temp. (°F)¹
'Nova Zembla'	Field	-10°	Feb. 6	* 2
	Poly house	10°	Feb. 19	-20
	Dark barn	25°	Feb. 26	-10
'Dr. H.C. Dresselhuys'	Field	-10°	Feb. 26	-20
	Dark barn	25°	Feb. 26	0
'Mrs. P. den Ouden	Field	-10°	Feb. 26	-5
	Dark barn	25°	Feb. 26	10

¹ Leaves held 2 hours at test temperatures.

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RECOMMENDATIONS

It may not be feasible or advisable to try to prevent internal leaf flooding in storage, since high humidity is needed to prevent leaf desiccation, especially while root balls are frozen. Leaves should be watched for flooding, especially after an extended period of rainy weather. Judicious ventilation for a day or two when the weather clears should cause the flooding to disappear. Ventilation should not be done when outside air is much below freezing, nor when root balls are frozen. If ventilation is not feasible, and leaves remain flooded, precautions should be made to prevent severe freezing, especially for several hours. Plants removed from storage in a flooded condition would be vulnerable to injury from a sharp freeze.

LITERATURE CITED

- 1. Kramer, P.J. 1966. Plant and water relationships. pp. 155-173. McGraw-Hill, New York N.Y.
- 2. Minshall, W.H. 1964. Effect of nitrogen-containing nutrients on the exudation from detopped tomato plants. Nature 202:925-926.

^{2*} indicates not damaged at -20°F.