

bility. The occurrence of such 3 banded types in the hybrid indicates that the enzyme GPI-2 has a dimeric subunit structure. This enzyme also has been reported to be a dimer in other studies (1, 3).

All interspecific hybrids between Friar plum and Flavorcrest peach had a 6 banded pattern in the PGM system, combining both parental types for PGM-1 and PGM-2 (Fig. 3). These patterns were consistent with the interspecific genotype of the hybrids. The observed multibanded patterns could be produced by hybrids with both peach and plum alleles at 2 loci, but not with only peach or plum alleles at either locus. Hybrids derived from plums with other PGM patterns, shown in Fig. 1, also may have 7 or 8 banded patterns. Additional crosses are needed to confirm that PGM is homozygous for the observed banding types in the parental cultivars.

This study has demonstrated that the interspecific hybrids between Friar plum and Flavorcrest peach can be identified with isoenzyme electrophoresis. In fact, either GPI or PGM electrophoresis would be sufficient

to identify the plum x peach hybrid progeny from the plum x plum progeny for the cultivars of plums and peaches tested. This is especially true for PGM, where the bands are unique to each species and there is no segregation in the F₁ genotypes. However, use of both systems is recommended for positive identification of hybrids.

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HORTSCIENCE 20(2):248-250. 1985.

Root Anaerobiosis, Root Respiration, and Leaf Conductance of Peach, Willow, Quince, and Several Pear Species

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Additional index words. *Cydonia oblonga*, *Prunus persica*, *Pyrus betulaefolia*, *Pyrus calleryana*, *Pyrus communis*, *Salix discolor*

Abstract. The effects of root anaerobiosis on root respiration and leaf conductance (kl) were determined in solution culture experiments. Respiration of feeder roots (<2 mm diameter) in air (21% O₂) of *Pyrus betulaefolia* Bunge, *Pyrus calleryana* Decne, *Pyrus communis* L. ('Old Home' x 'Farmingdale 97') and *Cydonia oblonga* Mill. 'Provence BA 29' was reduced by no more than 50% after 21 days of anaerobiosis. In contrast, root respiration of *Prunus persica* (L.) Batsch 'Lovell' was reduced by 80% with anaerobiosis, whereas that of *Salix discolor* Muhl. increased. Reductions in kl with anaerobiosis generally were more pronounced than reduction in root respiration when measured in air. Respiration rates of aerobically or anaerobically treated pear roots were inhibited by 25% to 50% when incubated in 0.5% O₂ compared to rates in air. More work is required in order to delineate the relationship of root respiration and kl with anaerobiosis.

Stomatal closure is an early plant response to flooding (12), often occurring within one

or several days after flooding (11, 12). Reductions in root respiration also have been shown to be one of the 1st plant responses to anaerobiosis (6). Although flooding reduces the transpiration rate of all except hydrophytic species, the exact underlying cause(s) are not completely understood (12). The O₂ requirement for active nutrient uptake has been documented (3); however, additional evidence suggests that the rate of water uptake is linked to rates of root respiration (8). Also, anaerobiosis induced xylem dysfunction has recently been shown to reduce water uptake by pear roots (2).

Flood tolerance may be due to a metabolic control over glycolysis (regulation of the Pasteur effect), and maintenance of the capacity for aerobic respiration after periods of O₂ deprivation (5). In a study with pear roots, Rowe (9) found a short-term increase in ethanol accumulation followed by a reduction after several hours of anaerobiosis, evidence of control over the Pasteur effect.

Our objectives were to study the effect of root anaerobiosis on root respiration and leaf stomatal closure, and to assess the relative merits of these parameters as flood tolerance indicators.

Two-year-old seedlings of *Pyrus betulaefolia*, *P. calleryana*, and *Prunus persica* and 2-year-old rooted cuttings of *P. communis* ('Old Home' x 'Farmingdale 97'), *Cydonia oblonga* (quince cv. Provence BA 29), and *Salix discolor* (pussy willow) were grown in sand for one growing season, and then transferred to a greenhouse during September. In the fall of 1980, plants were placed in 6 liters of nutrient solution and subjected to either aerobic (compressed air) or anaerobic (N₂ gas) solution culture treatments for various periods for up to 30 days. Excised feeder roots (<2 mm diameter) were placed in 38 cm³ vials filled with air.

Root respiration ($\mu\text{l CO}_2 \text{ g}^{-1} \text{ fresh weight}^{-1} \text{ hr}^{-1}$) was measured on 3 subsamples per plant with 3-4 replications per species for both treatments. After 3 to 5 hr of incubation at 22°C, CO₂ concentration was determined with a gas chromatograph equipped with a thermal conductivity detector. Previous experiments indicated that bacterial respiration was negligible, and CO₂ evolution was about linear from 0-5 hr after excision. Abaxial leaf conductance (kl) was determined during midday on 3 fully expanded leaves per plant on each of 4 replications (1, 2) with a ventilated diffusion porometer, consisting of a Triplett 220-6 microammeter and a lithium chloride Hydrodynamics 4-4832 humidity

Received for publication 18 Apr. 1983. Oregon State Agr. Expt. Sta. Tech. Paper No. 7147. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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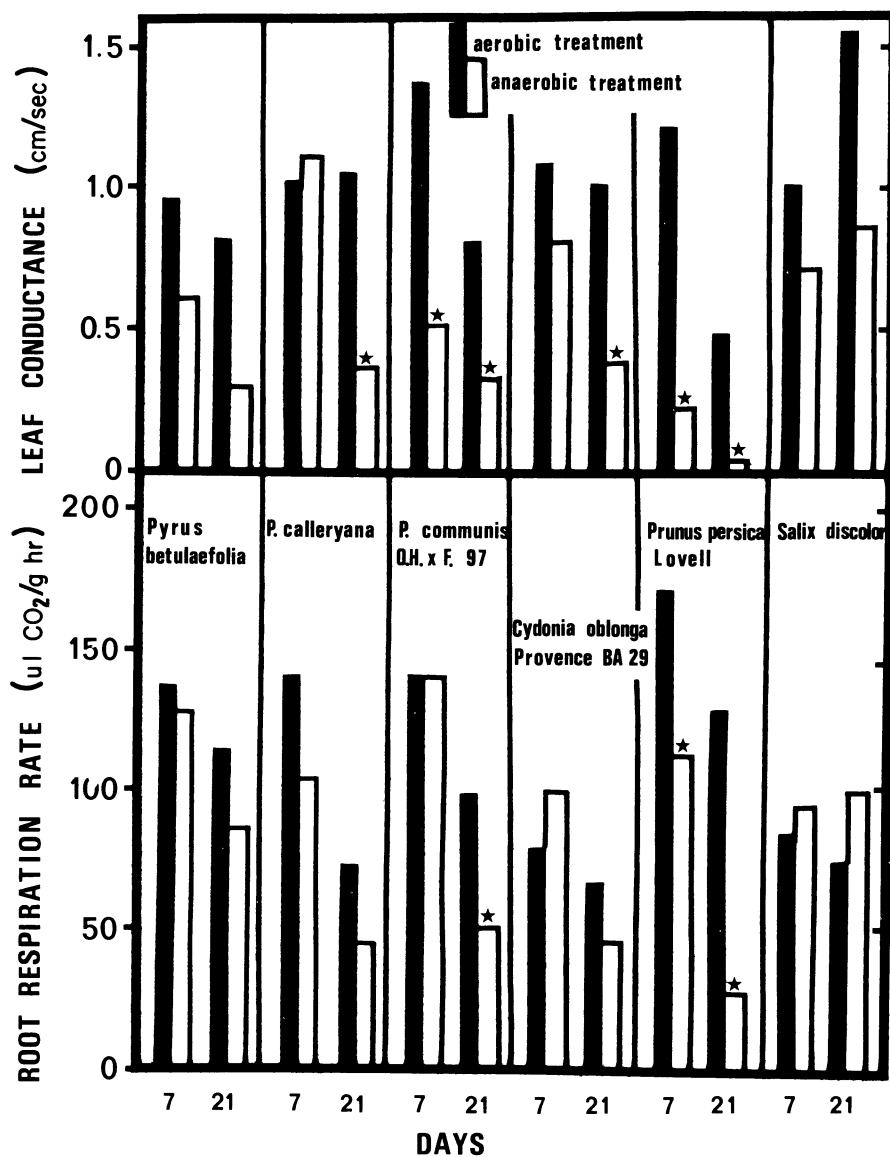


Fig. 1. Leaf conductance and root respiration rate of ungrafted *Pyrus*, *Cydonia*, *Prunus*, and *Salix* species 7 and 21 days after treatment imposition. Plants were grown in solution culture in the greenhouse. Root respiration was determined in 21% O₂. Significant difference (★) between treatments were determined for each species on each day separately by LSD, 5% level.

sensor with an aperture of 2.85 cm². The 1st experiment was analyzed as a completely randomized design.

During March and April, a 2nd experiment was conducted which was similar to the 1st except: 1) 'Bartlett' pear was grafted

on all pear rootstocks, 2) root respiration and leaf conductance were monitored on the same plants at 12 and 26 days, and 3) root respiration was determined in air and in the presence of 0.5% O₂ for both the aerobic and anaerobic solution culture treatments. Root

Table 1. Leaf conductance (kl) of 4 'Bartlett' grafted pear rootstocks subjected aerobic and anaerobic solution culture treatments.

Treatment	Treatment duration (days)	Leaf conductance in kl (cm s ⁻¹)			
		<i>P. betulaefolia</i>	<i>P. calleryana</i>	<i>P. communis</i>	<i>C. oblonga</i>
Aerobic	12	1.64	1.49	0.82	1.16
Anaerobic	12	1.35	0.72	0.25	0.98
Aerobic	26	0.77	0.75	0.58	0.78
Anaerobic	26	0.57	0.50	0.16	0.43
Main effects ²					
treatment		5%	NS	NS	1%
Duration		5%	1%	NS	NS
Interactive effects ²					
Treatment × duration		NS	5%	NS	NS

²Significance based on F values.

respiration data in this experiment were analyzed as a split-split plot design.

Anaerobiosis significantly reduced the respiration of roots in 21% O₂ (air) after 7 days for *P. persica* and after 21 days for *P. communis*, yet root respiration of *P. betulaefolia*, *P. calleryana*, *C. oblonga*, and *S. discolor* was not significantly affected (Fig. 1). In general, kl was more drastically reduced than root respiration on both dates. For example, the kl of *P. communis* was reduced after 7 days of anaerobiosis, whereas root respiration was not affected. Similarly, the respiration of *S. discolor* roots in the anaerobic treatments was increased numerically while the kl decreased, although in neither instance were the differences significant. Results of Fig. 1 indicated the necessity of monitoring root respiration of both treatments under conditions of low O₂ not just in air.

Since 'Bartlett' was grafted on all rootstocks in the 2nd experiment, differences in kl are directly attributable to the rootstock (Table 1). A significant anaerobic-induced decline in kl occurred for 'Bartlett' on *P. betulaefolia* and *C. oblonga*; however, a numerical decline occurred for 'Bartlett' on all rootstocks. Cloudy weather on day 26 probably is responsible for lower kl values compared to day 12. The treatment × duration interaction occurring for *P. calleryana* we believe is coincidental.

In reference to main treatment effects, root respiration was reduced significantly by anaerobiosis for all rootstocks, except *P. betulaefolia* (Table 2). In contrast, incubation in 0.5% O₂ significantly reduced respiration for all species, except *P. communis*. Quite unexpectedly, root respiration generally was higher on day 26 compared to day 12.

P. betulaefolia, *P. calleryana*, and *C. oblonga* maintained the capacity for aerobic respiration after 26 days of anaerobiosis (Table 2, See anaerobic × 21% O₂). In contrast, anaerobically treated *P. communis* manifested little increase in respiration rate in 21% O₂. All pear rootstocks, except *P. communis*, showed an increased capacity for root respiration on day 26 compared to 12. We are not confident that the 2 interactions with a significant F value are particularly meaningful (Table 2). A consistent relationship between kl (Table 1) and root respiration (Table 2) was not apparent beyond the observation that both factors tended to decline with anaerobiosis. In some instances, the reduction in kl with anaerobiosis appeared to be more strongly associated with root respiration measured in 0.5% O₂, than that measured in 21% O₂. In other instances, the latter was the strongest association.

The extreme and moderate sensitivity of *P. persica* and *P. communis* ('OH' × 'F 97'), respectively, and the relative tolerances of *S. discolor*, *P. betulaefolia*, *P. calleryana*, and *C. oblonga* were consistent with previous results involving soil flooding (1). No relationship was apparent between inherently high or low respiration rates and flood tolerance which is in agreement with other studies (4, 5).

Table 2. Effect of treatment (aerobic, anaerobic), incubation condition (21% O₂, 0.5% O₂) and treatment duration (day 12, 26) on root respiration on 4 'Bartlett' grafted pear rootstocks.

Treatment	Root respiration ($\mu\text{l CO}_2\text{g}^{-1}\text{hr}^{-1}$)					
	Incubation (% O ₂)	Duration (days)	<i>P. betulaefolia</i>	<i>P. calleryana</i>	<i>P. communis</i>	<i>C. oblonga</i>
Aerobic	0.5	12	40.0	41.7	52.7	44.7
		26	60.0	106.2	64.5	52.2
	21	12	72.1	99.5	87.6	105.5
		26	84.4	133.2	74.0	78.2
Anaerobic	0.5	12	41.7	30.2	40.3	26.7
		26	45.6	48.0	26.6	56.8
	21	12	62.4	35.6	53.4	48.7
		26	97.7	66.1	24.9	59.5
Main effect ¹						
Treatment			NS	1%	5%	5%
Incubation			1%	1%	NS	1%
Duration			5%	1%	5%	NS
Interactions ¹						
Treatment × incubation			NS	1%	NS	NS
Treatment × duration			NS	NS	NS	NS
Incubation × duration			NS	NS	NS	NS
Treatment × incubation × duration			NS	NS	NS	NS

¹Significance based on F values.

It has been suggested that O₂ transport from the shoot to the root is a factor responsible for the maintenance of aerobic root respiration in an anaerobic environment (4). This factor may explain high root respiration rates of *S. discolor* roots despite 21 days in an anaerobic environment (Fig. 1). The stem of *Salix* can conduct O₂ for limited distances to the root (7). Undoubtedly this characteristic contributed to the growth of *S. discolor* in flooded soil, whereas pear rootstocks merely survived (1). However, an anatomical study of aerobically and anaerobically treated *P. betulaefolia* and *P. communis*, ('OH' × 'F 97') revealed no evidence of aerenchyma (data not shown). The limited shoot and root lengths through which O₂ may diffuse in an intact woody plant (5) led Rowe and Beardsell (10) to conclude also that longitudinal air transport does not appreciably contribute to the flooding tolerance of quince and pear. In contrast, Rowe (9) explained the flood tolerance of pear by the possession of cytochrome oxidases, with a low Km for O₂ and the limitation of ethanol production by regulation of the Pasteur effect. Thus, although we did not detect evidence of aerenchyma, our data suggest that pear rootstocks maintain the capacity for high respiration rates, despite 26 days of anaerobiosis, and that pear roots are able to utilize O₂ effectively under low oxygen tensions. It also is entirely possible that anaerobic respiration substantially contributed to CO₂ evolution reported in the present paper. (We did not measure O₂ uptake.)

It has been suggested that root respiration (4, 6) and stomatal closure (1, 11) may serve as screening methods for assessing flood tolerance. Results present in this paper and previous field experiments (1) indicated that the inhibition of kl and root respiration offer some value as flood tolerance indicators. The procedure for determining root respiration is relatively time-consuming, since roots must be separated from the soil, then weighed and incubated for an appropriate time interval. A technique which measures a reduction in water uptake or water loss, such as porometry, is more expedient. However, one must be cognizant of atmospheric factors such as light level and relative humidity affecting kl measurements. Since the water conducting ability of pear roots is known to decline in response to root anaerobiosis (2), the reduction in kl of the anaerobic treatment is likely to increase on days of high vapor pressure deficit between the leaf and the atmosphere. This work suggests some relationship between the intensity of root respiration and kl, but a quantitative mathematical approach awaits further research.

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