Stomatal response to soil oxygen

New findings in stomatal response to oxygen could lead to changes in flood irrigation practices.

Oxygen levels in the voids between soil particles can vary over a wide range of concentrations. Flooding, recent incorporation of fresh organic matter, elevated soil temperatures, or combinations of these factors can lower soil-oxygen concentrations, either by stimulating rapid consumption of oxygen by microorganisms or by physically excluding oxygen from soil pores. Plant roots require adequate oxygen to respire and carry on various metabolic activities. When soil-oxygen availability to roots—as measured by the soil oxygen diffusion rate (ODR)—is low, plants develop a variety of stress symtoms. Unrelieved oxygen stress quickly damages plants and eventually reduces yields of most crops.

One mechanism resulting in plant damage involves the regulation of stomatal aperture. Stomata are the small pores in leaves and fleshy plant parts that allow gas exchange between internal leaf tissue and the atmosphere. The size of each pore is regulated by guard cells in response to light, water status of the plant, and various regulating chemicals in the plant. The importance of gas exchange through the stomata is linked to the need for atmospheric carbon dioxide (CO_2) for photosynthesis and for transpiration of water vapor.

Since low ODRs most often result from flooding, little attention has been paid to their effect on stomata. Stomatal response is generally regarded as a soil-water-related phenomenon. When soil-water availability is high, stomata are open; as soils dry, stomata begin to close. Therefore, one would expect stomata to be open in leaves of plants growing in flooded soil. Recent work, however, shows that this, in fact, is not the case.

Some plants have long been known to be more sensitive to soil aeration than others. Wilting, for example, commonly occurs shortly after soil-oxygen is excluded from roots of high-value cash crops like tomato or tobacco. Another interesting fact is that plants generally decrease water use when oxygen is excluded from the root zone—even if this exclusion is caused by flooding.

Several experiments conducted at the University of California, Riverside, have shown

Diffusive resistance, measured on tomatoes by Robert Sojka, indicates stomatal opening.

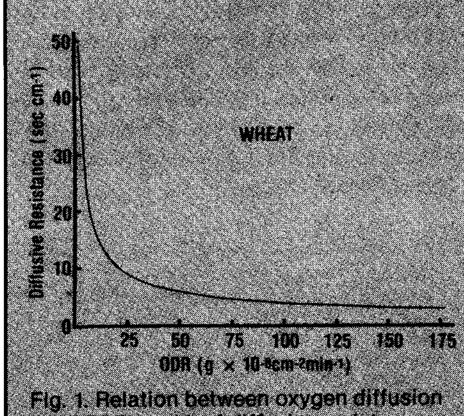


Fig. 1. Relation between oxygen diffusion rate (ODR) and leaf diffusive resistance.

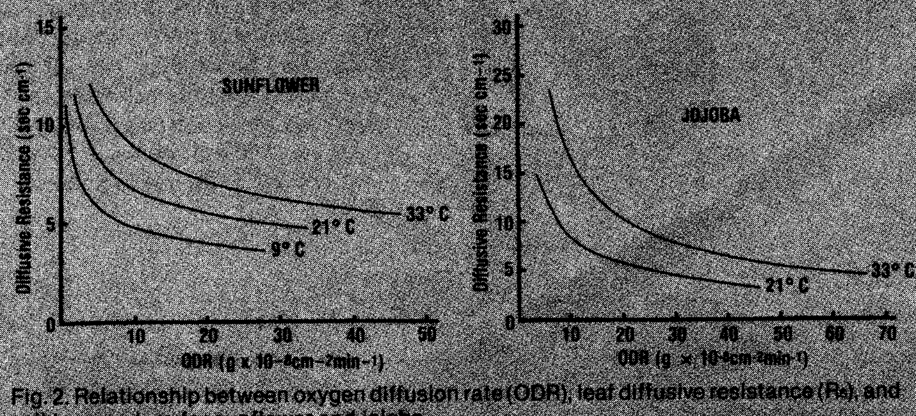


Fig. 2. Relationship between oxygen diffusion rate (ODR), leaf diffusive resistance (Rs), and soil temperature for sunflower and jojoba.

Lesion from *Phytophthora* stem infection.

Young euonymus shoot succumbing to aerial attack by *Phytophthora* sp.

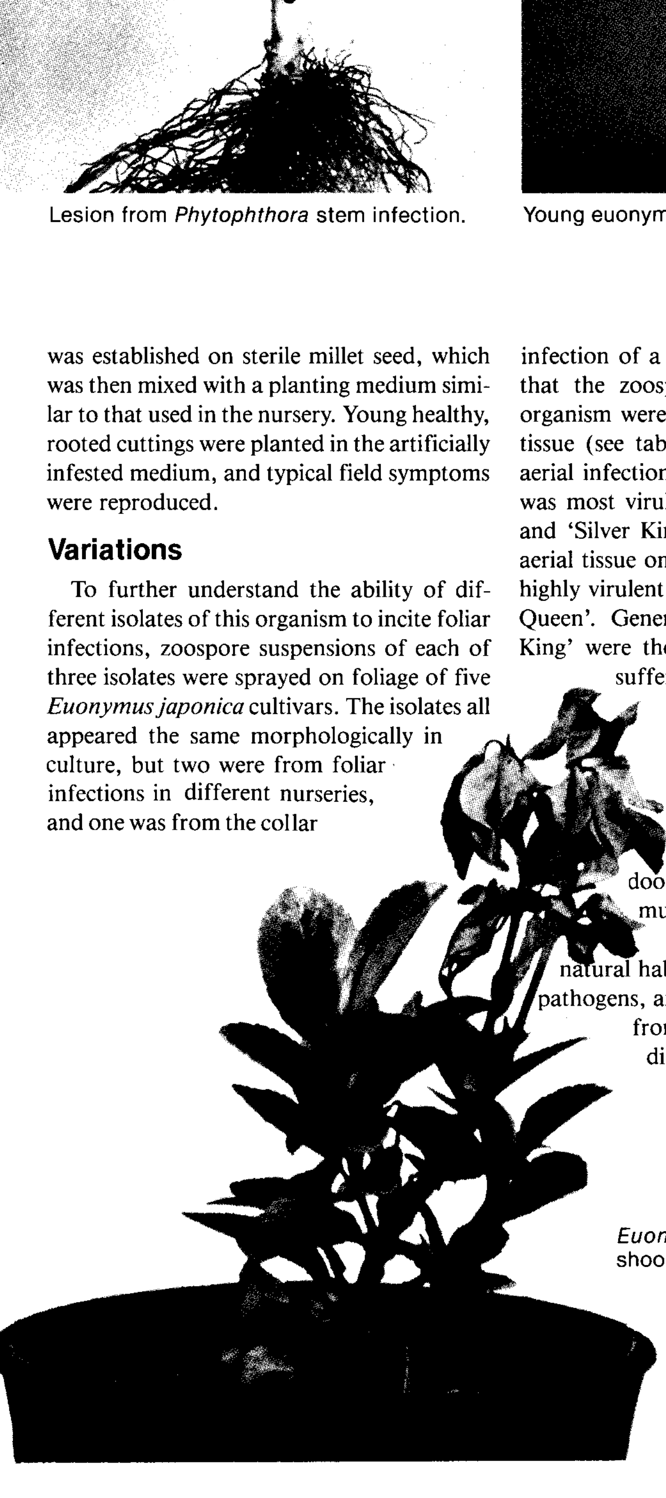
was established on sterile millet seed, which was then mixed with a planting medium similar to that used in the nursery. Young healthy, rooted cuttings were planted in the artificially infested medium, and typical field symptoms were reproduced.

Variations

To further understand the ability of different isolates of this organism to incite foliar infections, zoospore suspensions of each of three isolates were sprayed on foliage of five *Euonymus japonica* cultivars. The isolates all appeared the same morphologically in culture, but two were from foliar infections in different nurseries, and one was from the collar infection of a rooted cutting. It is obvious that the zoospores of the collar-infecting organism were unable to infect aerial shoot tissue (see table). The isolate (Ph-8) from aerial infections of 'Goldspot' in nursery A was most virulent on foliage of 'Goldspot' and 'Silver King', whereas the isolate from aerial tissue on 'Goldspot' in nursery B was highly virulent on all cultivars except 'Silver Queen'. Generally, 'Goldspot' and 'Silver King' were the most susceptible, and they suffered the most severe infections.

Control

The southern California coastal basin has an ideal climate for producing container-grown plants outdoors. As a result, the industry has mushroomed into major agricultural importance. The soil is a natural habitat for many soil-borne plant pathogens, and where watering is primarily from overhead sprinklers, foliage disease can become a problem.



Euonymus japonica 'Goldspot' shoot killed by *Phytophthora* sp.

Because foliar infections on *Euonymus japonica* have occurred primarily during periods of prolonged rain or mist and mild temperatures, pest managers in production nurseries have had success with regular applications of fungicides when unsettled weather conditions are forecast. Copper formulations similar to those used in preventive sprays against *Phytophthora* sp. causing brown rot on citrus have been effective.

To help control collar rot of rooted cuttings, it is important to take cuttings only from disease-free mother plants grown without overhead irrigation and treated regularly with suitable fungicides to ensure a disease-free condition. Fungicides, such as ethazol, that are selectively active against water molds have been used effectively as drenches after rooted cuttings have been transplanted into liner pots. When fungicides that are systemically active against *Phytophthora* sp. become commercially available, they could be used in the cutting flats sufficiently in advance of transplanting to greatly reduce the initial liner infections.

Randolph Keim is Superintendent of the South Coast Field Station, Santa Ana, and Research Associate, Department of Plant Pathology, University of California, Riverside; Laura J. Klure is Staff Research Associate, and George A. Zentmyer is Professor, Department of Plant Pathology, U. C., Riverside. *The valuable assistance of Elinor Pond, Department of Plant Pathology, Riverside, is acknowledged with thanks.*

Robert E. Sojka

Lewis H. Stolzy

that as the ODR of a soil decreases, stomata close, independently of other factors like soil-water status or light intensity.

Leaf diffusive resistance (R_s) is an indicator of stomatal aperture. When R_s is high, stomata are closed; when R_s is low, stomata are open. Figure 1 shows the effect of ODR on R_s for wheat grown in soil at equilibrium with gas mixtures of 0, 4, and 21 percent O_2. Soil temperatures were varied also to give 9°, 15°, and 21° C treatments. These two factors combined to create a range of ODRs. At low ODRs R_s increases sharply, indicating stomatal closure. This occurs despite the maintenance of uniformly favorable soil water status in all treatments.

Similar responses have also been found in tomato, cotton, sunflower, and jojoba. Figure 2 demonstrates the R_s increases of sunflower and jojoba in an experiment similar to the wheat experiment. Evidently, the R_s of both sunflower and jojoba responds to soil temperature. At high soil temperatures, the respiration rate of roots (O_2 demand) increases, as does competition for soil O_2 by soil microorganisms. Higher soil temperatures thus induce an oxygen shortage, which results in greater stomatal closure. Interestingly, crop damage caused by excessive soil water is usually more severe in warm weather than in cool weather. This follows from our results since stomatal closure due to flooding would prevent the normal transpirational cooling of plant tissues.

These findings have practical implications. When stomata are closed, we can expect not only heat stress to occur, but also photosynthesis to be reduced. These data may promote rethinking of the practice of flood-irrigating some crops, particularly on fine-textured soils, or when excessive canopy temperatures are likely. They also help us to better understand one mechanism of crop damage resulting from unwanted soil flooding.

Robert E. Sojka is Agronomist, Agricultural Research, Science and Education Administration, U.S. Department of Agriculture, Florence, South Carolina; and Lewis H. Stolzy is Professor of Soil Physics, Department of Soils and Environmental Sciences, University of California, Riverside. This article is a joint contribution of the Coastal Plains Soil and Water Conservation Research Center, USDA-SEA-AR, Florence, South Carolina, and the University of California, Riverside.

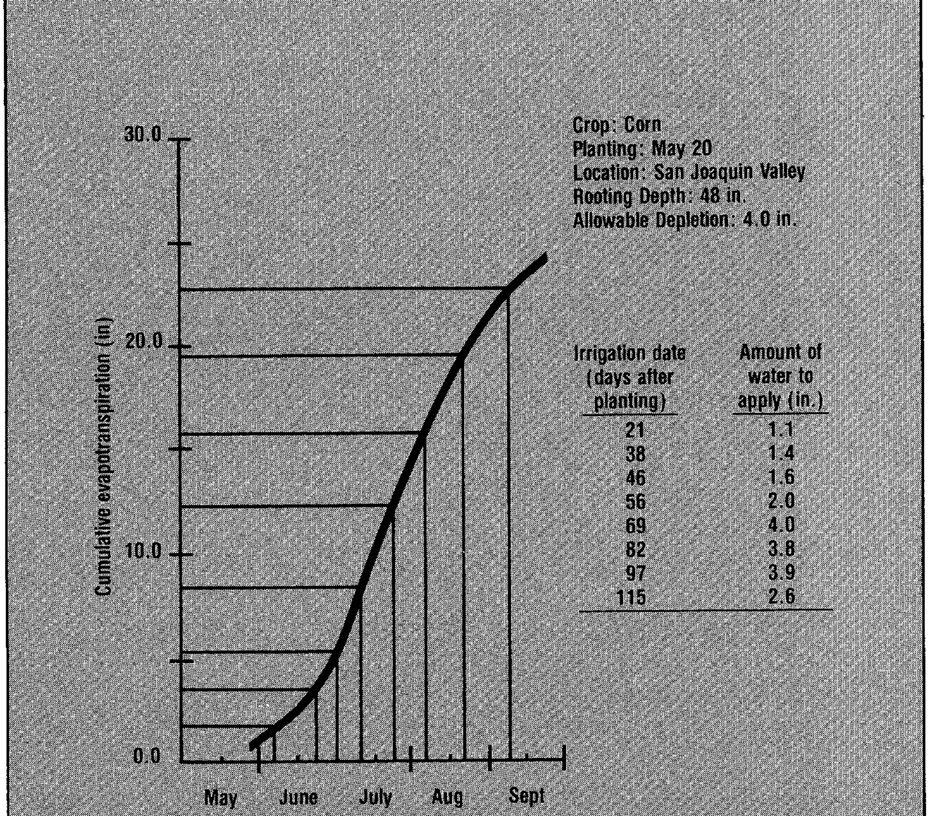


Fig. 1. An irrigation management program (IMP) for a corn crop on a medium-textured soil in California's San Joaquin Valley.

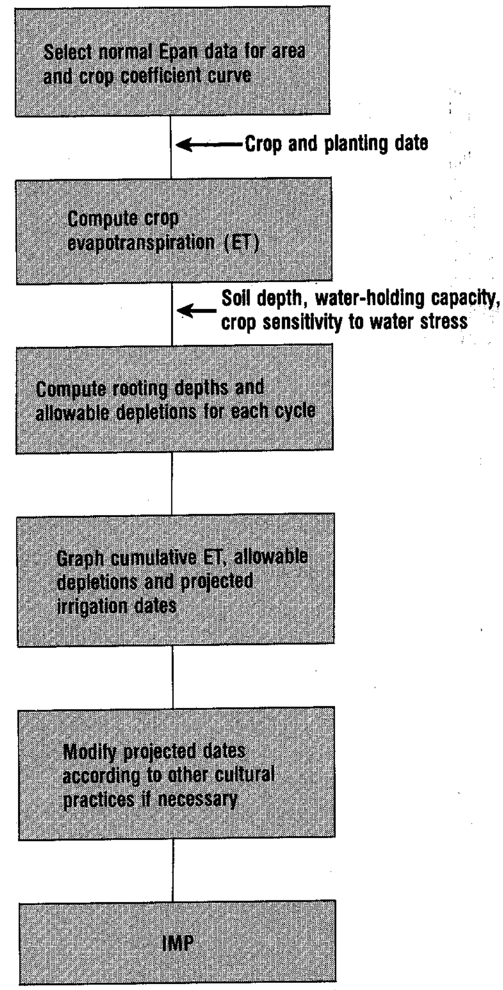


Fig. 2. Operation of IMP computer program.

about the depth of water actually applied at each irrigation; uncertainties in evaluating the crop rooting depth, soil water storage capacity, and allowable depletions; the spatial variability of soil water-holding characteristics within each field; uncertainties in computations of crop ET, particularly in the early growth stages; and the need to evaluate the effective rainfall on each farm.

This need for field checks and frequent calculations is perhaps one of the most important factors limiting broad acceptance of irrigation scheduling techniques among farmers. Although in some parts of the Central Valley, irrigation scheduling services may be contracted for, in many other areas where the apparent economic benefits do not justify the cost of such services, farmers do not have the time or expertise to make detailed water budget calculations and field checks. Therefore, despite significant efforts by various agencies and the University, adoption of detailed water budgeting techniques by farmers has not been widespread so far. A simplified approach to scheduling irrigations is needed that, at the same time, will have predictive value.

Irrigation management programs

If the ET data for a normal year are combined with the water-holding characteristics of a particular soil, an irrigation management program (IMP) may be designed that indicates when to irrigate and how much to apply under average or normal-year conditions. The example presented in figure 1 shows cumulative ET for any time after planting. The vertical distance between two adjacent horizontal lines represents the allowable depletion for each irrigation cycle. The irrigation date is determined by drawing the horizontal line to intersect the ET curve, and then a vertical line to the date line at the base of the graph.

This IMP, presented in tabular form or on a graph, is an easy-to-use, predictive tool that requires much less effort for irrigation programming by the farmer than do detailed water-budget calculations. If more accuracy is desired, the normal-year IMP provides an excellent base for irrigation scheduling: the ET curve is simply updated periodically with values from the current year and the irrigation dates changed accordingly. Once the appropriate IMP has been designed for a given soil-crop combination, it can then be used as a rational basis for irrigation scheduling with only periodic checks. In California these checks must be made more frequently at the start and end of the irrigation season, when unpredictable weather conditions may cause large year-to-year variations in ET rates.

The IMPs are valuable aids in predicting requirements for water, labor, and other essential inputs. They are also helpful in planning the date of the last irrigation so that expected winter rainfall will be stored within the root zone of next year's crop. And although they are based on the crop's being fully supplied with water, they are helpful in adjusting cropping patterns, planting dates, and other strategies when the preseason prediction is for a less-than-normal water supply.

It should be pointed out that under any irrigation scheduling method there are uncertainties in evaluating crop ET, the soil water-holding capacity, allowable depletion, and the volume of water applied at each irrigation and stored within the root zone, as well as its variability throughout the field. Thus the need for precise estimates of other parameters, including crop ET, may be questioned. Where soil water-holding capacity is low, water costs high, or crops very sensitive to water stress, the use of more sophisticated techniques for scheduling irrigations may be justified, however. Therefore, a computer model was developed so that IMPs could be designed for any crop-soil-management condition.

Designing IMPs

The irrigation scheduling model used in designing IMPs requires input of two parameters: crop evapotranspiration and allowable soil moisture depletion. Once these are