THE NATURE OF WATERLOGGING TOLERANCE OF LOBLOLLY PINE

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Abstract.--Loblolly pine seedlings develop many responses under waterlogging stress that are similar to adaptations to waterlogging in other higher plants. Some of the responses of loblolly pine seem to be less specialized than those exhibited by true wetland species. Lack of specialization is some cases seems to account for growth differences in relation to soil nutrient level and length and type of waterlogging. Screening for various adaptations appears to lave some potential for early progeny testing for wet site loblolly pine genotypes.

Additional keywords: gas exchange, iron-phosphorus complexes, morphology, anatomy and metabolism

Within its natural range loblolly pine is most prevalent on mesic sites but in the Atlantic and Gulf coastal plains individual trees frequently survive and grow well in shallow swamps, sloughs, wet flats, and other marginal wet sites. Consequently, many people including myself have theorized that wet site variants of loblolly pine exist throughout most of its range. However, scientific evidence to support this belief is lacking or, at most, is inconclusive.

Williams and Bridgewater (1981), in comparing loblolly pine families from deep peat and coastal plain sites found only a small family response to water regimes and that except for number of lateral roots, morphological traits and phytomass were statistically nonsignificant. Byram et al (1984) and Yeiser and Paschke (1987) reported that survival of some loblolly pine families was higher than others on wet sites. However, Yeiser and Paschke (1987) found no relationship between origin of ortet and family survival rates on wet sites. Topa and McLeod (1986a and b) found that a wet-site loblolly pine source from Robeson County, NC outgrew a dry-site source from Texas under waterlogging conditions and had a better internal ventilation system, but did not differ phosphorus uptake rates. At least one loblolly pine seed orchard exists in the South for improving loblolly pine performance on wet sites (i. e., the wet-site loblolly pine seed orchard of Federal Paper Board Company, Lumberton, NC).

In summary, genetic variation appears to occur in loblolly pine populations with regard to waterlogging tolerance but whether the variation large enough to be important in breeding and tree improvement programs has not been documented in the literature. Nor have there been sufficient comprehensive studies undertaker to determine the physiological and genetic basis of such variation.

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The traditional approach of using genetic tests and a seed orchard is obviously being used by Federal Paper Board Company and perhaps others that I am not aware of. If we are to expand our horizons in improving loblolly pine performance on wet sites three questions need to be addressed. They are: 1) is there significant variation among families with regard to performance on wet sites; 2) can physiological responses be correlated to performance in such a manner that they can be used for screening tools in selecting for waterlogging genotypes; 3) can physiological studies provide information that will help guide future breeding and tree improvement programs?

No conclusive answers are available at this time but preliminary results on loblolly pine family performances and physiological responses to waterlogging stress have been encouraging (see Shear and Hook in these proceedings).

Before proceeding, it seems necessary to briefly review what is know about morphological and physiological adaptations of higher plants to waterlogging stress.

ADAPTATIONS OF PLANTS TO WATERLOGGING.

Seed and Growth Dormancy

Plants that normally grow on wet sites generally differ from more mesophytic plants in many ways. Depending on the species, seed may germinate under water (rice) or may remain inactive until the water recedes below the soil surface (baldcypress and tupelos). Germination under water may be beneficial or hazardous depending on depth or duration of inundation (Kramer and Kozlowski 1979). Rice seed germinate under water and send up a coleoptile that must extend above the water level to provide an avenue for oxygen to diffuse to the seed before the germination process can proceed. It gains a growth advantage over many of its competitors by this mechanism. Baldcypress and tupelos seed remain dormant until flood waters recede, germinate, and go through a rapid height growth phase for one or two years. Presumably this rapid height growth phase is advantageous in getting their foliage high enough to be above the next flooding event. Other species do not leaf out until late May or early June hence they partially avoid early season stress by this strategy.

Morphology and Anatomy

Species such as baldcypress and tupelos develop a number of morphological and anatomical adaptations under flooding stress. They develop butt swell (hypertrophy), knees, and water roots. These adaptations appear to be beneficial for rapid growth but may not be necessary for survival. On the other hand, anatomical traits that accompany morphological developments appear to be necessary for life in such environments. Lenticel proliferation on the submerged stem and roots and the concurrent development of intercellular spaces within the stem and roots appear to be a vital part of a ventilation system necessary for growth in waterlogged environments. The ventilation system is so well developed in baldcypress and the tupelos that oxygen readily diffuses from the atmosphere through the stem and roots into the surrounding soil. Consequently, their roots essentially live in a micro-aerobic environment within soils that are devoid of oxygen and loaded with many reduced-toxic compounds.

Metabolism

Plants that live in waterlogged soils also have metabolic adaptations, not found in their dry land counterparts. Variations in basic metabolism among species seem to be related to the degree of waterlogging stress that each is capable of tolerating. Most plants tested to-date have shown that ethanol fermentation is the primary pathway for anaerobic metabolism under oxygen stress. Despite considerable efforts to understand how and to what degree anaerobic metabolism and internal aeration play in plant adaptation to waterlogged environments, their integrated role is still unclear.

It is known, for instance, that oxygen diffusion from the atmosphere to the roots in well adapted wetland plants, such as Spartina alterniflora, is not sufficient to explain their growth performance on some sites. Furthermore, there is evidence that anaerobic metabolism via ethanol production helps maintain the energy level in their roots high enough to support most active metabolic processes (Mendelssohn, McKee, and Patrick, 1980). In contrast, it is known that no cell growth and only limited protein production occurs in the absence of oxygen (Webb and Armstrong, 1983 and Vartapetian, 1987). Thus, the ventilation and the anaerobic metabolism systems appear to be intricately linked within plants that are adapted to wetlands but how is not clearly understood. During the past seven years, myself and several colleagues have sought answers to: 1) how does loblolly pine adapt morphologically and physiologically to soil waterlogging and 2) what characteristics of the soil and water regime trigger adaptive responses? The results of these studies will be summarized below.

GENERAL TECHNIQUES

Short-and long-term pot studies in growth chambers and in glasshouses and long-term studies (from one growing season to three growing seasons duration) in the soil tanks and in the field have been used to assess the response of loblolly pine to continuous waterlogging, seasonal waterlogging, periodic waterlogging, well drained conditions and natural water regimes on wet sites with and without phosphorus (McKee and Wilhite, 1986; Hook et al, 1983; DeBell et al, 1984; McKee et al., 1984; McKevlin et al., in press; Hook and McKevlin, 1987; Shear and Hook, 1987; and Hook et a, in prep). In addition, Hook and Denslow (1987) evaluated the response of four loblolly pine populations to two water regimes with and without phosphorus for one growing season in the soil tanks.

The soil tanks are structures at the Santee Experimental Forest Headquarters near Huger, South Carolina designed specifically to study the influence of soil waterlogging on tree species. These facilities consist of six tanks with dimension of approximately 6'x 6'x 6'. They are constructed such that water levels and flow rates can be maintained at desired levels and rates within or above the soil. The soil within the tanks are usually added so that they tend to mimic the structure of natural soil profiles on wet sites (see Hook, Stubbs, Langdon, and Brown, 1970).

RESULTS AND DISCUSSION

Most plant species develop outward evidence of waterlogging stress (Hook 1984) and hardwood species usually develop signs of stress rapidly under waterlogged conditions (Hook and Brown 1971). In comparison to hardwoods, loblolly pine responds to waterlogging stress very slowly. Except for a slight yellowing of foliage, eventual loss of some foliage and a relative slow growth rate, it does not express obvious signs of adapting or dying during the first year. Because of its slow response to stress, it is not possible to detect differences in family performance during the first year of waterlogging stress. The slow response time prolongs early screening trials.

Survival

Loblolly pine has remarkably high survival under continuous soil saturation, particularly, if inherent soil phosphorus levels are high or if sufficient phosphorus is added to the soil. Several studies have shown that first year survival under waterlogging stress will generally be 90 % or higher whether the experiment is done in pots in growth chambers or glasshouses, in the soil tanks, or in the field on wet sites. Even after three years in the field, survival averaged 83% on moderately wet sites and 70% on very wet sites. McKee and Wilhite (1986) found at age 10 years, loblolly pine survival was 73% on a poorly drained site but with added phosphorus or bedding plus phosphorus survival was 87%. Hence, early survival seems to have limited value in evaluating the tolerance of loblolly pine to wet sites.

Growth

of loblolly pine is generally decreased by soil waterlogging but its performance under waterlogged conditions is closely tied to the level of available phosphorus in the soil. When soil phosphorus level is adequate, loblolly pine growth rate under severe waterlogging stress may be as good as in well drained conditions. McKee and Wilhite (1986) found that fertilization with potassium and phosphorus, initially and nitrogen at age 6 years, increased height growth by 95% and volume growth by three to four fold. Since potassium had no effect on growth and the addition of nitrogen did not change the growth curve, they attributed most of the response to phosphorus effects. Hook and Denslow (1986) found large differences in growth rate of loblolly pine with and without phosphorus under two water regimes during the first growing season but could not find a family response to waterlogging and there were no significant family x phosphorus interactions.

Morphology, Anatomy, and Internal Aeration

Waterlogging results in a slight hypertrophy of the stem near the water level and lenticels develop on the roots and lower stem of loblolly pine seedlings. Occasionally some seedlings develop adventitious roots but the most common occurrence is for roots to die back to the main root or secondary roots and develop roots that are morphologically and anatomically different from the original roots. Some of the newly formed roots develop large aerenchyma zones distal to the apical meristem of the root. The aerenchyma zones are connected to the lenticels on the stem via intercellular spaces in the pericycle of the root and the cortex of the stem (McKevlin et al in press).

Gas exchange occurs rapidly through the aeration system (i.e., gas exchange between the atmosphere and the roots can be detected within one minute of changing the atmosphere around the shoots). Furthermore, the aeration status of the root can change completely from anaerobic to aerobic or vice-versa within 15-to-30 minutes in response to controlled changes in the atmosphere around the shoot. Despite the apparent rapid rate of gas exchange between the shoot and root, the system is not efficient enough to oxidize the rhizosphere of loblolly pine roots as do water and swamp tupelos (Hook et al, 1971; Hook and McKevlin, 1987).

Metabolism and Nutrition

Soil waterlogging reduces the uptake of all mineral elements except iron. If phosphorus is added to the soil prior to waterlogging, nutrient uptake increases but the concentration of nutrients still remains below the concentrations found in seedlings growing in well drained soils.

The solubility of iron increases significantly in waterlogged soils. Most wetland species avoid excessive uptake by oxidizing a portion of the excess iron on the outside of the root. But loblolly pine, because of its limited aeration system, oxidizes the iron inside the roots. Apparently, as the iron is oxidized inside the root, it complexes with phosphorus forming insoluble compounds. As a result, transport of phosphorus to the shoot is hindered. In soils that are inherently low in phosphorus, most of the phosphorus may be complexed in the root and result in a phosphorus deficiency in the foliage unless phosphorus is added.

When the roots of loblolly pine are placed in waterlogged or anaerobic environments they produce carbon dioxide, ethanol, and malate; end products of anaerobic respiration. Also, the enzyme alcohol dehydrogenase (ADH) becomes more active. The amount of end products formed and ADH activity level depends on the length of time the roots have been subjected to waterlogging stress and on the level of available soil phosphorus. For instance, DeBell et al (1984) found that carbon dioxide, ethanol, and malate production in loblolly pine roots was significantly higher with than without added phosphorus after one growing season in continuously flooded soils.

Phosphorus, also, appears to play an important role in regulating the leaf weight ratio of loblolly pine under a wide range of soil conditions. Hook et al (in prep.) found that the leaf weight ration was low in three waterlogged treatments and high in a well drained treatment without added phosphorus. But with phosphorus the leaf weight ratios were about midway between the extremes and did not vary among treatments. Hence, it seems that under waterlogged conditions phosphorus functions by allocating more of the photoassimilate into stem and foliage and under well drained conditions by allocating more photoassimilate into roots.

Under the stress of soil waterlogging, loblolly pine seedlings exhibit a number of well defined responses. Many of which have been identified previously in other plant species as adaptations to soil waterlogging. Therefore, we have been working under the hypothesis that if performance of families varied under waterlogging stress so would the adaptive responses.

Hence, it should be possible to correlate morphological and physiological responses to family performance. If this is possible, then key adaptations could be identified and used to screen for early indications of waterlogging tolerance among loblolly pine families (see Shear and Hook in these proceedings).

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