THE INFLUENCE OF ACID RAIN AND DROUGHT
ON EARLY GROWTH AND DEVELOPMENT
OF JACK PINE AND BALSAM POPLAR

by

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ABSTRACT

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Key Words: jack pine (*Pinus banksiana* Lamb.), balsam poplar
(*Populus balsamifera* L.), acid rain, drought, soil chemistry,
plant growth, development and physiology.

The influence of "acid rain" (watering with tap water acidified to pH 3.0) and drought on jack pine seedlings and balsam poplar cuttings growing in two different soil types was studied in a short-term greenhouse experiment. Changes in soil chemistry were assessed and a number of growth parameters and physiological processes measured.

Irrigation with "acid rain" led to rapid soil acidification. It resulted in decreased soil pH, cation exchange capacity and base saturation, and altered concentrations of the basic exchangeable ions; the level of $Al^{\cdot\cdot\cdot}$ increased, while the levels of $Ca^{\cdot\cdot}$, $Mg^{\cdot\cdot}$ and $K^{\cdot}$ decreased. There was a slight decrease in total soil organic matter and a slight increase in soil nitrogen. Drought generally enhanced the adverse effects of the soil acidification process.

"Acid rain" had a beneficial effect on seedling and cutting growth and development. Height and diameter growth, development of root surface area, production of aboveground and belowground biomass were stimulated by "rain" with pH 3.0. Seedlings and cuttings watered with "acid rain" also had lower water saturation deficit, lower diffusive resistance and higher transpiration rates. Changes in leaf chlorophyll fluorescence indicated slight stimulation of photosynthesis. Drought reduced seedling and cutting growth and development, but "rain" with pH 3.0 significantly reduced these adverse effects. Both tree species responded in a similar way to the stress factors. Plants performed better in the lighter soil because of better growth conditions. For early tree growth and development, "acid rain" was not directly harmful even when combined with drought.

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1. INTRODUCTION

The global atmosphere is changing continuously. Natural ecosystems, including forests, are exposed not only to a physical climate, but also to a modern chemical climate, which has the potential to alter health and productivity. Acid rain, this contemporary "evil", is caused mainly by emissions of sulphur dioxide (SO_2) and nitrogen oxides (NO_x). When released into the atmosphere, these substances can be carried long distances by prevailing winds and return to earth as acidic rain, snow or fog. A third strong mineral acid, although in small proportion relative to the other two, is hydrochloric acid (HCl). Rain formed in a non-polluting area should have a pH of about 5.5, but rains with low pH values fall in Europe, U.S. and Canada, often hundreds of kilometers from the major sources of air pollution (Kozlowski *et al*, 1991). Obviously, wet deposition is not just a regional problem. Moreover, acidic deposition is recognized as one of the most interdisciplinary environmental problems humankind has ever had. Soils and surface waters are affected; plant growth is retarded; ecosystems are changed; the biota in the lakes and rivers is changed; some organisms die; microorganism pathogens and soil fauna change their activity and living patterns; deterioration of buildings and valuable historical monuments takes place, and human health is affected (Acid rain, 1985).

In recent years a widespread decline of mature forests has been reported in many parts of the world. This problem is more serious in Central Europe (Ulrich and Pankrath, 1983; Postel, 1984; Falkengren-Grerup, 1989; Bressar and Salomons, 1991), but regions in North America showing similar symptoms are increasing rapidly and are already spread over the commercial forestlands in the eastern part of the United States (Puckett, 1982; Postel, 1984; Johnson, 1989; Bressar and Salomons, 1990; Tomlinson *et al.*, 1990). Deposition of atmospheric pollutants has been implicated as a main contributing factor in these declines (McLaughlin,1985; Fernandez, 1986; Fitter and Hay, 1987; Foster,1989, and others).

After years of intensive research on atmospheric deposition phenomena and their impact on forest ecosystems contradictory evidence has been developed. At present only a few questions have good answers and too much is unclear. The negative changes in the forests of Europe and North America continue and still there are uncertainties surrounding the mechanisms and the specific causes for these changes. Our knowledge is insufficient to explain all these changes and to suggest adjustments in forest management decisions which might reduce both the possible effects of atmospheric deposition and forest decline. Although today we know much more, we are still near the starting point. Acid rain remains a forestry dilemma. One can find scientists claiming that there is no significant effect whatsoever (Skelly, 1989; Woodman, 1987), and acid rain actually benefits forests through some fertilizing effect associated mainly with its nitrate (NO_3) content (Morrison, 1984; Lee and Weber, 1979; Raynal *et al.*, 1982; Troiano *et al.*, 1982). Still others claim an adverse effect (Wood and

Bormann, 1974; Tamm and Cowling, 1977; Evans *et. al*, 1978; Ferenbauch, 1976; Hindawi *et al.*, 1980; Johnston *et al.*, 1982; Olszyk *et al.*, 1989). The problem is complex, because all of the pollutant stresses are likely to be interactive with other natural stresses, but in exactly what way, or to what extent is unknown. According to Fernandez (1986) we still do not understand:

1. The mechanisms of atmospheric deposition effects responsible, if any, for the modern deterioration of forests under a variety of environmental conditions.

2. The degree of deposition of gaseous pollutants, trace metals, particles, cloud moisture and organic compounds in most remote forest areas.

3. The dose-response relationships for most pollutants under ambient field conditions in forest ecosystems. More importantly, we have a very poor understanding of the effects on forests of interactions between individual pollutants and between pollutants and natural stresses.

4. The natural and the air pollution stress factors responsible for the unexplained regional forest deterioration.

In order to determine the role of anthropogenic factors in forest decline, the major mechanisms of pollutant action have to be defined more clearly. Continuing research is required in:

(1) rigorous experimentation under controlled conditions to reproduce tree injuries by the mechanisms implied in a particular hypothesis;

(2) the manner in which pollutants interact with natural stress factors to affect physiological functions in trees;

(3) long-term ecosystem scale studies of responses of forests to pollutant deposition.

In order to further clarify the relationship between anthropogenic and natural stress factors, the influence of acid rain and drought on two valuable forest tree species was investigated.

2. LITERATURE REVIEW

2. 1. THE ACID RAIN SITUATION

Although widespread damage from air pollution has not been observed in North America, isolated incidence of *Picea rubens* and *Abies fraseri* decline at high elevations at the Appalachian Mountains, regional hardwood damage or decline in conifer growth (Jagels *et al.*, 1986; McLaughlin *et al.*, 1987; Hornbeck *et al.*, 1986; Cox *et al.*, 1989; Turner and Tingey, 1990) and chlorosis of foliage in *Betula* sp. (Addison, 1989) have been documented. If we assume that 20 kg/ha/yr of wet deposited acid is a threshold for "significant" pollutant deposition, then approximately 15 million ha of forests are exposed to excessive acid deposition (Pearson and Percy, 1989). Between 1970 and 1977, annual man-made emissions of SO_2 in the U.S. declined about 10% due to abatement strategies, and in 1977 the total man-made emission of SO_2 was estimated to be about 29.9 million tons. During the same period, however, emissions of NO_x increased by about 17%. It is estimated that over the next 20 years annual emissions of man-made SO_2 will increase slightly to about 30 million tons, but NO_x emissions, in contrast, are expected to increase significantly to about 27 million tons per year (NAPAP, 1982). This is a potential danger for Canada as well, because the eastern part of the country receives 2.2 million tons per year (50% of the 1980 pollution level) from the U.S. Moreover, 46% of the soils and bedrock in Canada has low potential to reduce the acidity of atmospheric deposition and another 21% has moderate potential. These lands also contain aquatic ecosystems extremely vulnerable to acidic deposition (Acid rain, 1988). Recently, increasing evidence has been provided that acidification of winter precipitation in eastern Canada can be due as much to NO_3 as to SO_4 . Nitrates are also believed to be major components in the so-called spring snowmelt shock, but the effects of this phenomenon on forests have not been studied yet (Kelly *et al.*, 1990). Environmental effects are expected to continue and even get worse due to delayed acidification of aquatic and terrestrial ecosystems (Galloway,1989).

2. 2. ACID RAIN AND FOREST GROWTH

The first efforts to assess the effects of acidic precipitation on forest growth were made in Scandinavia, and they all used observational methods. Jonsson (1977) developed a method to examine the statistical correlation of *Pinus sylvestris* and *Picea abies* growth (as measured by annual ring widths for the period 1910 - 1965) with the intensity of increasing acid precipitation initiated in 1950 in southern Sweden. The analysis did not enable the author to conclude that acid rain was the cause of the registered reduced growth. Likewise, acid rain was not eliminated as a cause, and the analysis did not support any alternative explanations for the poorer growth observed.

In a very similar study no consistent regional growth differences were observed in Norwegian forests (Abrahamsen *et al.*, 1977). Moreover, less productive sites, poor vegetation types and shallow soils did not appear to be more sensitive to acidification.

The results from three Finnish National Forest Inventories gave some support to the hypothesis that atmospheric changes and/or changes in the nitrogen compounds in acid deposition have increased forest growth in southern Finland (Bressar and Salomons, 1990). Statistical tests show that shift in growth response for the periods 1901 - 1920 and 1954 - 1973 corresponds with the increase in acid rain and air pollution (Puckett, 1982).

In the U.S. the forest regions subject to the most acidic precipitation are located in the Northeast. In a comprehensive study of production and biomass of the northern hardwood forests conducted at the Hubbard Brook Experimental Forest in New Hampshire, Whittaker *et al.* (1974) observed a significant decline in growth from 1956 - 1960 to 1961 - 1965. The period of growth decrease was coincident with a period of increasing acidity in precipitation and inferred that this may be responsible for the decrease in productivity.

By using tree-ring analysis Cogbill (1977) concluded that no correlation of forest growth and acid rain could be established for eastern North America. On the basis of observational study in the Adirondack Mountains, Le Blanc *et al.* (1987) also stated that it may be very difficult to document anomalous pollution induced decreases in mixed forests growing on more fertile soils in eastern North America.

With observational studies failing to yield consistent and conclusive evidence that acid rain does or does not appreciably decrease forest growth, attention was turned to experimental approaches.

In a long-term experiment, conducted in Sweden, the periodic volume growth of *Pinus sylvestris* was little affected, while there was considerable ground vegetation kill (Tamm, 1976; Tamm *et al.*,1977). Some years later it was noted that while on unfertilized plots basal area increments increased with acid (H_2SO_4) application, on fertilized plots the reverse was true. The negative effects on the fertilized plots were attributed to the acid rain, because it was assumed that here the primary nutrient deficiencies were satisfied (Tamm and Wiklander, 1980, after McLaughlin, 1985).

In a similar long-term experiment in Norway, growth of *Pinus sylvestris* was unaffected, height and diameter growth of *Picea abies* slightly decreased and height growth of *Betula verrucosa* was stimulated by the acid rain treatment (Abrahamsen *et al.*, 1976, Abrahamsen, 1980, after Morrison, 1984).

In other long-term experiments fertilized and unfertilized plots of 18-year old *Pinus sylvestris* trees were irrigated below the canopy with H_2SO_4 in dosage of 50-150 kg/ha/yr. After six years a negative correlation between treatment acidity and basal area growth was found on the fertilized plots. Growth response to acidification was positive on the unfertilized plots. Increased nitrogen uptake was considered a probable cause of the positive growth responses. It was noted, however, that in the long term, results are complicated by changes in nutrient availability in the soil associated with the direct effects of high acidity on soil fungi, bacteria, and competing understory vegetation, as well as by the absence of contact with the canopy by the simulated rainfall (Tamm and Wiklander, 1980, after McLaughlin, 1985).

In similar Norwegian experiments, acid rain with pH 2.0, 2.5 and 3.0 increased growth of *Pinus sylvestris* after four years, but this was followed by a significant growth reduction by pH 2.0 in the fifth year.

Growth of *Picea abies* was reduced and of *Betula verrucosa* stimulated (Abrahamsen *et al.*, 1977; Tveite and Abrahamsen, 1980, after McLaughlin, 1985).

In another long-term Norwegian experiment with *Pinus contorta* and *Picea abies* no negative impact of acid rain was detected after three years. In fact *Pinus contorta* exhibited 20% stimulation of height growth and *Picea abies*, 15% (Tveite and Teigen, 1976, after Smith, 1990). Usually increased growth was attributed to the fertilizing effect of added sulfur and nitrogen (McLaughlin, 1985; Smith, 1990).

A number of short-term experiments have also produced contradictory evidence about the effects of acid rain on growth. Height growth of seedlings of *Pinus halepensis* decreased when exposed to acid rain with pH 3.1 for one growing season (Matziris and Nakos, 1978). On the other hand, *Pinus banksiana* and *Picea glauca* showed no statistically significant reduction in growth rate even when the acid rain applied had pH as low as 2.6 (Abouguendia and Bascak, 1987). Acid mist with pH 2.9 reduced the average radial increment of spruce as calculated for the period 1970 - 1985 (Jagels, 1986). Acid rain with pH 3.0 and more did not affect growth of four broadleaf species: *Quercus alba*, *Carya ovata*, *Fagus sylvatica* and *Fagus grandifolia* (Jensen and Dochinger, 1989), and also of *Picea rubens* and *Pinus taeda* (Seiler and Paganelli, 1987). Stimulation of photosynthesis and growth of *Pinus strobus* and *Pinus taeda* seedlings was reported as well (Reich *et al.*, 1987; Hanson *et al.*, 1988), but it was suggested that this was just a temporary effect due to the increased nitrogen fertilization.

While at present forest growth seems little or not at all diminished, it is possible that conditions for growth have been altered in such a way, that in the future growth will be affected.

2. 3. ACID RAIN AND FOREST TREE PHYSIOLOGY

It has been established that acid rain may cause adverse metabolic changes and injuries in plant tissues and cells. The effects may be "contact", i.e. deriving mainly from direct contact of the pollutants with plant surfaces, and "non-contact", i.e. produced secondarily as a result of change of some other environmental component. Tamm and Cowling (1977) give a good summary of the potential effects of acidic precipitation on vegetation (Table 2. 1).

The hydrogen ion can directly affect a number of biochemical processes and reactions, including cell wall elongation and enzyme activity. These effects are plausible physiologically because the cell sap acidity is normally maintained within a relatively narrow pH range, necessary for maintenance of enzyme configuration and reactivity (Devlin, 1966). While plant cells have buffering mechanisms to deal with excess acidity, the limits to which those systems may be stressed by ionic changes imposed by losses of Ca^{++} and Mg^{++} and gains of H^{+} during canopy reactions with acid rain are not known (McLaughlin,1985). Strong acids may also substantially change the properties of cell walls, including accelerating the loss of cell osmotic potential (Heath, 1980).

Foliar damage might include cuticular damage, interference with normal functioning of guard cells and poisoning of plant cells after diffusion of acidic substances through the stomata or cuticle (Tamm and Cowling, 1977). It may also cause leaching of mineral nutrients from leaves (Reich *et al.*, 1988) and lead to decreased photosynthetic efficiency or

Table 2.1. Potential effects of acidic precipitation on vegetation (after Tamm and Cowling, 1977).

Direct Effects:

1. Damage to protective surface structures such as cuticle.
2. Interference with normal functioning of guard cells.
3. Poisoning of plant cells after diffusion of acidic substances through stomata or cuticle.
4. Disturbance of normal metabolism or growth processes without necrosis of plant cells.
5. Alternation of leaf and root exudation processes.
6. Interference with reproductive processes.
7. Synergistic interaction with other environmental stress factors.

Indirect Effects:

1. Accelerated leaching of substances from foliar organs.
2. Increased susceptibility to drought and other environmental stress factors.
3. Alteration of symbiotic associations.
4. Alteration of host-parasite interactions.

abnormal water relations (Kozlowski *et al.*, 1991). Development of necrotic spots on hardwoods (with spot diameter increasing with increasing of mist acidity from 5.5 to 2.3), curling and shortening of leaf blades and even death of leaves and whole plants under extreme treatment (pH 2.3) have been reported (Wood and Bormann, 1974). Similar results for conifers are also reported (Jacobsen and Van Leuken, 1977, after Morrison, 1984). There is some evidence (in experiment with *Populus* sp.) that "very young" leaves seemed less affected, but this is still not fully understood (Evans *et al.*, 1978). Foliage of evergreen conifers particularly is less well buffered against acidic pollution than that of broadleaf species (Pylypec and Redmann, 1984), but there are studies that show no harmful effects even when there is interaction with O_3 (Reich *et al.*, 1986a, 1988).

Forest trees may be especially vulnerable to acid rain in the seedling stage. In studies with controlled environments, acid rain simulants had significant direct or indirect impacts on seed germination, radicle elongation and seedling growth and development.

In a number of experiments acid rain with pH 3.0 or less was found to cause root necrosis (Huttermann and Ulrich, 1984) or reduced root growth (Matzner *et al.*, 1986; Lee and Weber, 1979; Squire *et al.*, 1987; Neufeld *et al.*, 1985) and reduction of fine root system (Ulrich and Pankrath, 1983; Tomlinson *et al.*, 1990). Acid rain reduced root growth not only when it was with low pH, but also when the doses were increased (Cizkova,1987).

Acid mist with pH 2.7 and 3.4 stimulated root growth of *Pinus jeffreyi* (Temple, 1988). While biomass production of *Picea abies* was not affected by acid rain with pH as low as 2.5 (Ogner and Teigen, 1980), both total biomass production and height growth were reduced at pH 2.0 for *Liquidambar styraciflua*, *Platanus occidentalis* and *Robinia pseudoacacia*

(Neufeld *et al.*, 1985). In an experiment with 11 woody species treated with acid rain having pH 3.0, 3.5 and 4.0, shoot growth was stimulated by at least one treatment for four species (Lee and Weber, 1979). Lee *et al.* (1990b) demonstrated that when acid rain with pH 4.0 was applied, shoot growth was more sensitive to Al than was root growth; root growth was more sensitive to O_3.

Altered plant-water relations can result from either diminished capacity of the plant to take up water from the soil or a loss in capacity to control water loss from foliage. Decreased uptake can be caused by a reduction in biomass of fine roots (Tomlinson *et al.*, 1990). Reduced root function can be due either to direct toxicity induced by soil chemical changes associated with increased soil acidification or to reduced translocation of carbohydrates from pollution damaged shoots (Mooney *et al.*, 1990). Several studies indicate that direct toxicity to fine roots is a result of soil acidification, which causes a build-up of aluminum and iron to toxic levels and changes significantly the $Al^{\cdot\cdot\cdot}$: $Ca^{\cdot\cdot}$ ratio (Ulrich and Pankrath, 1983; Huttermann and Ulrich, 1984; Rost-Siebert, 1984, after McLaughlin, 1985; Tomlinson *et al.*, 1990).

In addition to direct effects on root biomass, soil acidification may result in changes in availability of cations, particularly $Ca^{\cdot\cdot}$, necessary for proper root growth and normal physiological function. Physiological and histological studies support the idea that adequate calcium levels are important for growth of meristematic tissues and proper membrane development and stability. In general, stresses that reduce the capacity of aboveground plant systems to produce photosynthate at a rate required for growth and development of these tissues result in reduced allocation to root systems and a consequent decline in root vigor (Tomlinson *et al.*, 1990).

Changes in cuticular integrity and changes in stomatal function by pollutants may alter plant capacity to regulate transpirational water loss. Acid rain and associated pollutants can alter leaf surface characteristics, principally through weathering or chemical alteration of cuticular waxes (Shriner, 1983, after McLaughlin, 1985). Only a small fraction of the acid precipitation intercepted by a stand of vegetation will adhere to plant surfaces, the remainder being lost to the soil. Pollutants retained on leaf surfaces in this way become indistinquishable from gaseous pollutants dissolving in water films adhering to leaf surfaces (Fitter and Hay, 1987). At present neither the mechanisms (whether reduced wax production or increased weathering) nor the physiological significance of cuticular alteration by acid rain have been adequately characterized (McLaughlin, 1985). However, the rate of movement of pollutant species into the leaf tissues will depend on the resistance of the cuticle and the degree of surface damage inflicted by the pollutant (Fitter and Hay, 1987). The results of studies with conifers in Scandinavia suggest that cuticular changes observed in the field may occur only as a result of a longer term of exposure of foliage to pollutant combinations rather than single pollutants such as acid rain (Fowler *et al.*, 1980, Hornvedt *et al.*, 1980, after McLaughlin, 1985).

Increased uptake of potentially toxic elements such as aluminum and iron is an additional apparent result of increased exposure of soil and foliage to acid deposition. Because movement of the more mobile metals such as aluminum occurs in the transpiration stream, these elements can be expected to be concentrated near sites of evaporative loss of water and, hence, build-up in and around the guard and subsidiary cells of the stomates may occur. Accumulation of metals in these tissues may lead to altered physiological control of stomatal action and potential changes in leaf-water balance. Increased stomatal resistance has been reported for peach seedlings, which also showed decreased root volume when grown in nutrient solution with aluminum concentrations 46 mg/l (Horton and Edwards, 1976).

It has also been found that there is an inverse relation between pollutant exposure and stomatal resistance. This is interpreted as a dose-related loss of stomatal control. More rapid transpiration rates from excised polluted leaves also indicate this and perhaps an increased cuticular permeability. As a result there was an increase in plasticity of tissues, indicating that pollutants induced cell wall loosening. All these changes enhance the sensitivity of trees to drought and winter dessication (Barnes *et al*, 1990). It has been also reported that transpiration in spruce seedlings can be reduced markedly even by low levels of Al in nutrient solutions (Vogelman, 1982).

There is a strong negative correlation between pollutant concentration and root : shoot ratios. This results primarily from a progressive reduction in root growth and some increase in shoot growth. A reduction in root : shoot allocation may predispose a plant to drought stress (Becker and Neighbour, 1988).

Photosynthesis is one of the most fundamental metabolic processes of forest ecosystems and is the primary determinant of growth and biomass accumulation. The rate of photosynthesis of mature trees frequently is given within the range 10 - 200 mg of CO_2 taken up per gram of dry weight per day (Kozlowski *et al*, 1991). The rate is extremely variable and is influenced by genetic differences, season of the year, time of day, position within the crown of the tree, age of foliage, climate, and edaphic factors (Mooney *et al.*, 1990; Kozlowski *et al.*, 1991).

Studies with a wide variety of agricultural and herbaceous species under controlled environmental conditions have indicated that air contaminants must be added to the list of environmental variables that can potentially alter the rate of photosynthesis (Mooney *et al*, 1990).

The basic process of photosynthesis requires the entrance of CO_2 in the leaf. Since this entry takes place mainly through the stomata, the factors responsible for their opening or closing are also to a great extent responsible for the rate of photosynthesis. The process is also dependant on the content of chlorophyll, an essential pigment for this process.

Little evidence has been presented on the influence of acid rain on photosynthesis of forest trees. Researchers have reported increased photosynthesis (Ferenbauch, 1976; Reich *et al.*, 1987; Lee *et al.*, 1990b), no effects (Neufeld *et al*, 1985; Reich *et al.*, 1986a; Seiler and Paganelli, 1987) or reduced photosynthesis (Lee *et al.*, 1990a).

In an experiment with *Eucalyptus globulus*, net photosynthesis decreased for three experimental levels of acid rain: pH 3.5 applied for 4h, pH 2.2 applied for 4h, and pH 2.2 applied for 8h. After three to four days plants recovered only in the first experimental level, i.e. pH 3.5 applied for 4 h. This was attributed to morphological changes in the leaves and alteration of stomatal and mesophyll resistances (Valentini *et al*, 1989).

Reich *et al* (1986a) exposed 2-year-old *Acer saccharum* and *Quercus borealis* seedlings to combinations of acid rain and O_3. While O_3 alone caused significant decreases in net photosynthesis, acid rain had no effect on photosynthesis, and no interactions of the two pollutants were observed.

In an experiment conducted by Taylor *et al.* (1986) the rates of CO_2 assimilation and transpiration on a per gram needle dry weight of 1-year-old *Picea rubens* seedlings were not influenced by mist and rain chemistry or soil type. The authors speculated that the decline in *Picea rubens* stands may be due either to change in whole-plant allocation of carbon resources, or to a direct toxic effect in the rhizosphere.

Interactions between soil properties, plant nutrition and acid deposition were important in assessing the impact of acid rain on *Pinus strobus* seedlings (Reich *et al.*, 1987). Acid rain and soil type had a strong interaction in determining pine response. Acid rain caused increased growth and net photosynthesis as a result of nitrogen fertilization from the rain simulant. The extent of the fertilization response was inversely correlated with nitrogen availability in each soil. Similar results were also reported by Hanson *et al.* (1988). When working with 1-year-old *Liriodendron tulipifera* seedlings, Roberts (1990) found that acid rain had a greater impact on physiological activity than did O_3 or drought. Seedlings treated with pH 3.0 rain simulant exhibited significant reductions in carbon exchange rate, stomatal conductance and xylem pressure potential relative to trees treated with pH 5.5 rain.

Chlorophyll fluorescence has been proved to be an easy, fast and precise method for determining the effects of different stress factors on photosynthesis (Havaux *et al.*, 1988; Bolhar-Nordenkampf *et al.*, 1989; Lechner and Bolhar-Nordenkampf, 1989; Ogren, 1990). The decline in Fv/Fp (Fv - variable fluorescence, Fp - fluorescence at the peak) fluorescence is associated with an equal decline in Fv/Fm (Fm - maximal fluorescence). Fluorescence is related also to a similar decline in maximum quantum yield of O_2 evolution, suggesting that the decline in Fv/Fp ratio represents damage to photosystem II attributable to photoinhibition (Ogren, 1988). There is also a strong correlation between Fm and CO_2 uptake (Toivonen and Vidaver, 1988).

Chlorophyll content of *Pinus banksiana* was not affected by acid rain even when the rain had a pH as low as 2.6 (Abouguendia and Bascak, 1987). However, chloroplast structural injury has been reported with *Pinus contorta* var. *latifolia* tissues by Jaakola *et al.* (1980, after Morrison, 1984) who demonstrated an increase in spectral reflectance which was related to decreases in chlorophyll, although correlations with photosynthetic rate were not successful. This shows once again the complex character of this process and its relationships with a number of internal and environmental factors.

It has been proposed that acid precipitation could adversely affect soil biota and biotic processes in the forest floor and underlying mineral soil such that, over the long run, site fertility could be diminished. Tamm (1976), for example, proposed a hypothetical model relating increase in acid deposition in a soil of high C : N ratio with a decrease in microbial activity in the A_0 and A_1 horizons and ultimately with less nitrogen available to trees. It is plausible that acid rain could influence forest growth by such a mechanism.

It is generally acknowledged that both soil fauna and soil microflora are influenced by soil acidification. Microorganisms which are important in carrying out reactions essential or stimulatory to plant growth, in contributing to soil structure, in decomposing organic matter, and in destroying various environmental pollutants are influenced by pH.

Preliminary results from decomposition experiments have been generally inconsistent. Significant decreases in decomposition in acid treated soils beneath young *Pinus sylvestris* plantations (Baath *et. al,* 1979, 1980 after Morrison, 1984) have been reported. Addition of acid to incubated *Pinus sylvestris* raw humus (Tamm, 1976) and to a New York *Quercus/Pinus* ssp. sandy loam in vitro also caused decrease in CO_2 evolution (Fransis, 1982). At present the possibility that under natural conditions reduced pH would be of small importance for biological activity, and the possibility that further acidification could lead to significant reductions in leaf litter decomposition, ammonification, nitrification and denitrification and thus affect nutrient cycling in forest ecosystems are both supported (Morrison, 1984).

The rhizosphere and symbiotic microrganisms are very important in nutrient relations in forest ecosystems. It is well known that a soil pH of about 5.0 is optimal for many mycorrhizal fungi and that alkaline soil pH is associated with poor mycorrhizal formation (Smith, 1990). However, laboratory evidence regarding mycorrhizal activity is inconclusive. Acid rain of pH 3.0 reduced infection of pine seedlings (Shafer *et al.,* 1985, Stroo and Alexander, 1985), but acid treatment with pH 2.4 increased ectomycorrhizal infection (Shafer *et al.,* 1985). Acid rain reduced mycorrhizae, caused their deformation and disturbed the symbiotic equilibrium. It was suggested that symbiotic fungal activity may be restricted by nitrogen deposition. Decreased ectomycorrhizal colonization of spruce as a result of atmospheric nitrogen input has also been reported (Alexander and Fairley, 1983). Moreover, according to Mohr (1985) there appears to be no phenomenon connected with the new forest decline which cannot be explained by the hypothesis of mycorrhiza damage due to excessive nitrogen.

2. 4. ACID RAIN AND SOILS

Perhaps the most frequently mentioned potential impacts of acid deposition are those related to soil acidification and base leaching. As a result of studies in the Solling forests in Germany, evidence has been presented that soil acidification causes release of the accumulated negatively charged sulfate ions into the seepage water which in turn increases the loss of the positively charged cationic nutrients from the soil (Tomlinson *et al*, 1990). The chemistry of acidification involves replacement of base cations (K^{+}, Ca^{++}, Mg^{++}, Na^{+} etc.) on exchange sites on particle surfaces with H^{+} ions, and at lower pHs with solubilized Al^{+++} ions. Trivalent Al^{+++} released in acidic soils, is not a tree nutrient and is more strongly absorbed on the exchange sites on soil particles than the lower valence nutrient cations Ca^{++}, Mg^{++} and K^{+}. As Al^{+++} enters solution as a result of acid inputs at pH 4.2 or less, Al^{+++} and H^{+} become the predominant cations, displacing the nutrient cations which are gradually leached from the soil with SO_4'' and NO_3' leading to nutrient impoverishment (Ulrich and Pankrath, 1983; Morrison, 1984; Tomlinson *et al*, 1990). The resulting increased molar ratios of aluminum to calcium and aluminum to magnesium have a deleterious effect on root systems - the length and vitality of root systems decrease, calcium and magnesium deficiencies are induced (Ulrich and Pankrath, 1983; Tomlinson *et al*, 1990). It is important, however, that the potential losses of nutrients be considered in relation to: (1) the available pools of nutrients in the soil and vegetation; (2) natural leaching losses from internal acid production by trees and microorganisms; (3) rates of resupply of nutrients from mineralization of soil organic matter and weathering of minerals, and (4) nutrient uptake and incorporation into woody biomass (Johnson *et. al*, 1982). On the other hand, positive effects occur where nitrogen inputs in acid rain represent a significant addition to available nitrogen in soils (McLaughlin, 1985).

From the viewpoint of practical soil management, it may be that no subject is of greater significance than "site sensitivity", although there would seem to be no general agreement among experts. One group holds that more fertile soils with higher pH are subject to greater change and hence are more "susceptible"; another holds that even minor change (of pH or base status) of infertile soils might render them unfavourable even for undemanding species. In one of the earlier treatments of this subject Wiklander (1974), taking into account factors related mainly to acid/base status, postulated that: (1) there would be no "adverse effects" on calcareous soils; (2) noncalcareous clays of pH > 6 would be moderately affected; and (3) such effects would be considerable in noncalcareous sandy soils of pH > 6, nil to slight for cultivated soils of pH > 5 and very slight to slight for acidic soils of pH < 5. Later he concluded that very acid soils are far less sensitive to acid rain as they are already adjusted to this condition by soil formation and therefore are more stable. However, factors contributing to sensitivity such as the difference in lime potential, the buffer capacity of the soil profile and the fraction of the water body that reacts with the soil, the anion retention capacity and the base leaching are also believed to be involved and are considered to be very important (after Morrison, 1984).

2. 5. WATER STRESS AND PLANTS

It has been shown that environmental variables, such as light intensity, temperature and relative humidity may have significant influence on the responses of plants to air pollutants (Barton *et al.*, 1980; Norby and Kozlowski, 1982; Taylor and Selvidge, 1985; Jensen and Roberts, 1986; van Hove *et al.*, 1990; Kozlowski *et al.*, 1991).

Water is essential as a constituent of physiologically active cells, as a reagent in photosynthesis and hydrolytic processes, and as a solvent in which solutes move from cell to cell. An essential role of water is maintaining turgor of guard cells and photosynthetically active cells. The importance of high turgor to photosynthesis cannot be overemphasized because the rate generally declines when leaves are only slightly dehydrated. When trees are subjected to drought and then rewatered, the rate of photosynthesis often fails to return to normal for a very long time because of damage to stomata and chloroplasts. Furthermore the loss of growth frequently attributed to competition or root injury is often traceable to decreased absorption of water leading to desiccation of the tree crown.

A complication in evaluating the physiological mechanism of pollution injury is that factors such as light, water, temperature, and mineral nutrition affect the response of plants to pollutants. Still another complication is that in the field more than one pollutant often is responsible for the injury. Moreover, the environment may be considered as the sum of all external forces affecting tree growth. Inasmuch as tree growth is an integrated response to physiological changes regulated by a complex of many fluctuating and interacting environmental factors it is difficult to evaluate the contribution of a single stress factor to growth (Kozlowski, 1979; Mooney *et al.*, 1990).

Plant water stress affects almost every aspect of plant morphology and physiology and has a dramatic impact on cell, tree and stand productivity. Water stress occurs when water content decreases to a level that affects physiological processes - usually it is caused by drought, but it develops also whenever transpiration exceeds water absorption long enough to cause reduced plant turgor.

At a cellular level it is known that water stress can reduce cell enlargement and growth, inhibit enzyme activity, affect membrane conformation and influence other physiological processes. At the level of a tree it can decrease root growth as a proportion of plant growth (Squire *et al.*, 1987); reduce diameter and height growth (Kozlowski, 1979); and reduce the ability of the tree to resist other stresses. Water stress also reduces transpiration (Squire *et al.*, 1987; Kozlowski, 1979; Kozlowski *et al.*, 1991) and photosynthesis (Smith, 1990; Kozlowski *et al.*, 1991). It causes changes in the amounts of secondary compounds and influences the timing and rate of other physiological processes (Kozlowski, 1979; Grieu *et al.*, 1988; Smith, 1990; Kozlowski *et al.*, 1991). At the stand level water stress can cause a decrease in leaf area, an increase in mortality and replacement of one species by another (Smith,1990; Kozlowski *et al.*, 1991).

Physiological processes have paramount importance in controlling tree growth, but they all are strongly dependant on the environmental conditions. Thus, environmental stresses often set in motion a sequential and complicated series of metabolic disturbances, rather than a single change in only one process such as phothosynthesis, as is sometimes supposed. However, growth and development of trees depend fundamentally on synthesis of carbohydrates and their immediate use or conversion to storage forms. In recent years a great deal of attention has been given to two different specific biochemical pathways of photosynthesis, C3 and C4 photosynthesis. Unfortunately, virtually all woody plants, with their C3 photosynthesis, are less well adapted than C4 plants to undergo stress conditions of drought and higher temperatures. However, the relation of photosynthetic capacity to growth is complicated, mainly because photosynthetic capacity varies greatly among species, varieties, clones and provenances, depends on the seasonal pattern of photosynthesis, the duration of growth, the relation of photosynthesis to respiration and the partitioning of photosynthate within the tree (Kozlowski, 1979).

Tree growth is central to the whole issue of the effects of acid deposition on forests. It may be considered the end product of a chain of processes both within the tree itself and in the ecosystem at large. Yet relatively few studies which employed methods that might establish growth reduction or non-reduction directly have been undertaken. Also, there have been relatively few attempts to establish such relationship indirectly (Morrison, 1984). Nevertheless, inasmuch as the forestry values at stake are overwhelmingly economic, the necessity for establishing reduction or non-reduction of growth inequivocally is not diminished. It may be argued that present forest growth may seem a little diminished, but conditions for growth are being altered in such a way that, in the future, growth will probably be affected.

3. MATERIALS AND METHODS

In order to examine more closely the effects of the two stress factors, namely acid rain and drought, on two forest tree species, a short-term experiment was performed in the greenhouse of Lakehead University, Thunder Bay, Ontario.

3. 1. MATERIALS

3. 1. 1. Soils

For the purposes of the experiment balsam poplar and jack pine were planted in two soils.

The soils, a "heavy" and a "light" one, were taken from George Burke Park, Thunder Bay. The different soil types, represented mainly by C horizon, were chosen by eye and by finger texture analysis. The soils were transferred to the greenhouse of Lakehead University, where they were sterilized with a "Lansa" soil sterilizer to prevent contamination. In order to unify the microflora of the growing media, each soil was inoculated with about 10% from the other. It was considered that this will not change the soil properties. Prepared in such a way the soils were used in the experiment.

The soils were characterized by texture, pH of the soil solution, organic matter, cation exchange capacity and percentage base saturation, and amount of exchangeable ions before and after the treatments. The following methods were used.

1. Mechanical analysis for determining the soil texture was completed following the standard procedure described by Carmean and Vanson (1982).

2. Soil pH was determined in water solution and in 0.01M $CaCl_2$ solution using a standard method and a pH-meter (Carmean and Vanson, 1982).

3. Total organic matter was estimated by the loss-on-ignition method (Carmean and Vanson, 1982). In addition to this samples of 10 g of each soil type were given to the Instrumental Laboratory of Lakehead University for analysis. Carbon, hydrogen and nitrogen content were determined with CEC 240-XA elemental analyzer, using a standard combustion method.

4. Cation exchange capacity and percentage base saturation were determined following the methodology described by Carmean and Vanson (1982).

5. Exchangeable ions. Ammonium acetate extractions, representing the soils were prepared according to the Wilde *et al.* (1979) procedure and were submitted to the Instrumental Laboratory of Lakehead University for analysis. The amount of exchangeable $Al^{\cdot\cdot\cdot}$, $Ca^{\cdot\cdot}$, $K^{\cdot}$ and $Mg^{\cdot\cdot}$ was determined by ICP - AES (Inductively Coupled Plasma Atomic Emission

Spectrometry) in a Jarrell-Ash ICAP 9000, using an instrumental method designed for this application.

The mechanical analysis showed that the "heavy" soil contained 60.23% sand, 37.00% clay and 2.77% silt. Based on these data it was classified as sandy clay. The "light" soil contained 78.64% sand, 15.00% clay and 6.36% silt and was classified as sandy loam.

Initially the light soil was more acidic than the heavy soil. The values of soil pH in H_2O and in 0.01M $CaCl_2$ were 6.35/5.30 for the light soil and 7.50/7.20 for the heavy soil.

Before the treatments the soils were medium to high humic. The heavy soil contained 4% organic matter and the light soil, 6%. Initially the organic matter in the heavy soil contained more carbon and less hydrogen and nitrogen (.99% C, .21% H, .01% N) than the organic matter in the light soil (.85% C, .25% H, .03% N). Also, the heavy soil had a larger C : N ratio at 184 than the light soil at 33.

Initially the heavy soil had cation exchange capacity of 12 meq/100 g soil, and the light soil, 14 meq/100 g soil. The percentage base saturation was 71 for the heavy soil and 57 for the light soil.

Before the treatments the amount of the exchangeable ions was as follows:

	Heavy soil	Light soil
$Al^{\cdot\cdot\cdot}$,ppm	0.3137	1.713
$Ca^{\cdot\cdot}$,ppm	382.7	72.84
$K^{\cdot}$,ppm	12.103	16.315
$Mg^{\cdot\cdot}$,ppm	40.44	18.74

3. 1. 2. Plants

Two forest tree species, jack pine (*Pinus banksiana* Lamb.) and balsam poplar (*Populus balsamifera* L.), were used in the experiment.

The balsam poplar cuttings were taken from an experimental plantation on Lakehead University campus, Thunder Bay, Ontario. A northern provenance (Pickle Lake area, Lat. 51° N, Long. 90° W) was represented by clones 101, 102, 118, 142, 149, 151, and a southern provenance (northern Wisconsin, Lat. 46° N, Long. 90° W), by clones 220, 253, 261, 266, 268, 269. In early April, 1992, before budbreak, branches from ramets of these clones were cut, put in black plastic bags and stored in a refrigerator at a temperature of about 3°- 4° C .

The jack pine seeds were obtained through the Ontario Tree Improvement Council. The seeds from a northern provenance (34-23-0-01), originated from Armstrong, Ontario (Lat. 50° N, Long. 89° W), and were collected on March 22, 1984. The seeds from a southern provenance (44-25-0-02) originated from the Matawin forest near Thunder Bay, Ontario (Lat. 48°15′ N, Long. 89°26′ W) and were collected on February 3, 1988. They were stored in a refrigerator at a temperature of about 3°- 4°C as well.

3. 2. METHODS

The experiment (Table 3. 1) was established using a completely randomized design in the main greenhouse of Lakehead University.

Table 3.1. Experimental design.

Species and provenances	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
	drought	control	drought	control	drought	control	drought	control
Jack pine (northern)	6	6	6	6	6	6	6	6
Jack pine (southern)	6	6	6	6	6	6	6	6
Balsam poplar (northern)	6	6	6	6	6	6	6	6
Balsam poplar (southern)	6	6	6	6	6	6	6	6

Note: 6 is the number of replications.

Ninety six pots (diameter 30 cm) were filled with light soil and 96 with heavy soil. Ninety six pots (48 with light soil and 48 with heavy soil) were planted with jack pine and 96 pots (48 with light soil and 48 with heavy soil) were planted with balsam poplar.

On June 1, 1992, 30 jack pine seeds were put in each pot and covered with sand. After germination the seedlings were thinned to 15 per pot. At this stage they were sprayed with "No Damp" to prevent damping-off. Two weeks later the seedlings were thinned to six per pot.

Cuttings about 15 cm long were prepared from the balsam poplar branches. Three cuttings were planted in each pot. After cutting establishment, the cuttings were thinned to one per pot. All clones were evenly distributed and later represented in each tratment. However, we did not keep track of clonal differences because they were out of the scope of this study.

All pots were marked with provenance descriptions, and cuttings and seedlings were raised under the climatic conditions maintained automatically in the main room of the greenhouse: humidity 50%, day temperature 24 C and night temperature 18 C, and photoperiod 18 h. The pots were watered by hand to field capacity once a day. During this period some of the pots filled with heavy soil dried out more than others and occasional cracks were formed in the soil through which water ran. This was fixed in time and the plants were not damaged.

The "acid rain" was prepared by adjusting the pH of tap water with concentrated sulphuric (H_2SO_4) and nitric (HNO_3) acids. When 1 mL of each acid was added to 20 L of water, the pH of the solution was 3.07. In order to obtain solution with pH 5.19, 0.3 mL of each acid were added to 25 L of water. The acidity was determined with a pH-meter, using buffer standard

4663. The "acid rain" was prepared immediately before the treatments and its acidity was checked with a pH-meter at application.

Drought was induced by creating drought cycles . The plants to which drought was assigned did not receive water or "acid rain" for seven consecutive days. It was considered, and later confirmed through the experiment, that this period was long enough to induce drought stress effects without killing the plants.

On August 18, 1992, after the seedlings and the cuttings were established, treatments were randomly assigned to the pots according to the design outlined in Table 3. 1. All the pots were marked with treatment and replicate numbers. "Acid rain" was prepared and the plants were treated for seven days. Starting on August 24, 1992 six drought cycles were created during the treatment period, which lasted 11 weeks. Each drought cycle lasted seven days and was followed by seven days of rewatering with water with pH 3.0 or 5.0 respectively.

3. 2. 1. Assessment

Soil characteristics at the end of the experiment were assessed with the same methods described in 3. 1. 1.

To assess the influence of the stress factors on plants the following parameters were measured.

I. Growth:

1. Seedling and cutting height were measured at the beginning, in the middle and at the end of the treatment period.

2. Root collar diameter of the pine seedlings and stem diameter of the poplar cuttings were measured with calipers after harvesting.

3. Root surface area was determined with a Rhizometer, following the standard procedure of Day (1985).

4. Oven dry weight. After harvesting, the belowground and the aboveground parts of the plants were separated, dried in an oven at about 80 C for 24 h and weighed on analytical scales.

5. Plot volume index (PVI) of Marx (Marx *et al.*, 1977) was calculated for the pine seedlings according to the formula

PVI = (mean seedling volume) x (number of surviving seedlings),
where
mean seedling volume = (height) x (root collar diameter).

II. Physiological state:

1.Water saturation deficit was determined by the disk method of Weatherley (Slavik, 1982) for both tree species.

2. Transpiration and diffusive resistance were measured for the poplar with a Li-Cor 1600 porometer during a drought cycle at the beginning and at the end of the treatment period.

3. Chlorophyll fluorescence of pine and poplar leaves was measured with a Bio Monitor (made in Sweden) during a drought cycle at the end of the experiment. The apparatus, known as Plant Stress Meter, was developed by Gunnar Oquist and Roland Wass, Department of Plant Physiology, University of Umea, Sweden and is designed to provide fast and accurate measurement of chlorophyll fluorescence. Long used as a probe for photosynthesis, the chlorophyll in the membranes of chloroplasts emits red fluorescence of which a part, the induced or variable chlorophyll fluorescence is responsible for changes in photosystem II activity. From this it follows that any stress applied to green plant tissue which directly or indirectly affects photosynthetic metabolism is likely to change the

yield of this fluorescence. The variable chlorophyll fluorescence is closely correlated to the availability of the acceptor molecules. It has also been shown that the photochemical efficiency of photosystem II is proportional to the Fv/Fm ratio (Fm - maximal fluorescence characteristic of open reaction centres) when non-photochemical. A decrease in Fv/Fm ratio is indicative of the photoinhibition of photosynthesis and of stress impact on the enzymatic phases of the carbon reduction cycle. Thus, through changes in chlorophyll fluorescence, information on the function of photosystem II and hence on the photosynthesis of the plant is obtained.

In order to have precise measurements an adaptation period of 45 minutes in the dark was allowed immediately before the measurements. A photon flux density of 3, which means 200 μmol photons/m/s for a running time of 2 seconds, was used. These parameters were chosen because it was considered that Fv/Fm is roughly proportional to the quantum yield of photon flux density 3. Running time of 2 seconds is optimal for this flux density.

3. 2. 2. Statistical Analysis

The experiment was conducted using a completely randomized design, and its general linear model was

$$
\begin{aligned}
Y_{ijklm} = {} & \mu + S_i + P_j + A_k + D_l + SP_{ij} + SA_{ik} + SD_{il} + PA_{jk} + PD_{jl} + AD_{kl} \\
& + SPA_{ijk} + SPD_{ijl} + SAD_{ikl} + PAD_{jkl} + SPAD_{ijkl} + \varepsilon_{(ijkl)m}
\end{aligned}
$$

where

Y_{ijklm} - the yield associated with the mth experimental unit in the ith level of factor S (soil type), the jth level of factor

P (provenance), the kth level of factor A (acid rain) and the lth level of factor D (drought)

μ - the overall mean

S_i - the effect of the ith level of factor S

P_j - the effect of the jth level of factor P

A_k - the effect of the kth level of factor A

D_l - the effect of the lth level of factor D

SP_{ij} - the effect of the interaction of the ith level of factor S with the jth level of factor P

SA_{ik} - the effect of the interaction of the ith level of factor S with the kth level of factor A

SD_{il} - the effect of the interaction of the ith level of factor S with the lth level of factor D

PA_{jk} - the effect of the interaction of the jth level of factor P with the kth level of factor A

PD_{jl} - the effect of the interaction of the jth level of factor P with the lth level of factor D

AD_{kl} - the effect of the interaction of the kth level of factor A with the lth level of factor D

SPA_{ijk} - the effect of the interaction of the ith level of factor S with the jth level of factor P and the kth level of factor A

SPD_{ijl} - the effect of the interaction of the ith level of factor S with the jth level of factor P and the lth level of factor D

SAD_{ikl} - the effect of the interaction of the ith level of factor S with the kth level of factor A and the lth level of factor D

PAD_{jkl} - the effect of the interaction of the jth level pf factor P with the kth level of factor A and the lth level of factor D

$SPAD_{ijkl}$ - the effect of the interaction of the ith level of factor S with the jth level pf factor P, the kth level of factor A and the lth level of factor D

$\varepsilon_{(ijkl)m}$ - the random effect of the mth experimental unit in the ijklth treatment combination

The sources of variance and the degrees of freedom for each tree species are shown in Table 3. 2.

Table 3 .2. Sources of variance and degrees of freedom in the experiment.

Sources of variance	Degrees of freedom
Soil type (S)	1
Provenance (P)	1
Acid rain (A)	1
Drought (D)	1
SP	1
SA	1
SD	1
PA	1
PD	1
AD	1
SPA	1
SPD	1
SAD	1
PAD	1
SPAD	1
Exp. error	80
Corrected total	95
Mean	1
Total	96

3.2.2.1. Soil characteristics. When determining the soil characteristics we used two replications for each treatment. The sources of variance and the degrees of freedom in this case are shown in Table 3.3.

3.2.2.2. Plant characteristics. The rate of transpiration and the diffusive resistance were measured in six consecutive days, and the fluorescence in consecutive days. The sources of variance and the degrees of freedom in these two cases are shown in Table 3.4 and Table 3.5 respectively. The general linear model for these parameters was

$$\begin{aligned} Y_{ijklmn} = \mu &+ T_i + S_j + P_k + A_l + D_m + TS_{ij} + TP_{ik} + TA_{il} + TD_{im} + SP_{jk} + \\ &+ SA_{jl} + SD_{jm} + PA_{kl} + PD_{km} + AD_{lm} + TSP_{ijk} + TSA_{ijl} + TSD_{ijm} + \\ &+ TPA_{ikl} + TPD_{ikm} + TAD_{ilm} + SPA_{jkl} + SPD_{jkm} + SAD_{jlm} + PAD_{klm} + \\ &+ SPAD_{jklm} + TSAP_{ijkl} + TSPD_{ijkm} + TSAD_{ijlm} + TPAD_{iklm} + TSPAD_{ijklm} \\ &+ \varepsilon_{(ijklm)n} \end{aligned}$$

where

Y_{ijklmn} – the yield associated with the nth experimental unit in the ith level of factor T (time), the jth level of factor S (soil type), the kth level of factor P (provenance), the lth level of factor A (acid rain) and the mth level of factor D (drought)

μ – the overall mean

T_i – the effect of the ith level of factor T

S_j – the effect of the jth level of factor S

P_k – the effect of the kth level of factor P

A_l – the effect of the lth level of factor A

D_m – the effect of the mth level of factor D

TS_{ij} – the effect of the interaction of the ith level of factor T with the jth level of factor S

TP_{ik} – the effect of the interaction of the ith level of factor T with the kth level of factor P

TA_{il} - the effect of the interaction of the ith level of factor T with the lth level of factor A

TD_{im} - the effect of the interaction of the ith level of factor T with the mth level of factor D

SP_{jk} - the effect of the interaction of the jth level of factor S with the kth level of factor P

SA_{jl} - the effect of the interaction of the jth level of factor S with the lth level of factor A

SD_{jm} - the effect of the interaction of the jth level of factor S with the mth level of factor D

PA_{kl} - the effect of the interaction of the kth level of factor P with the lth level of factor A

PD_{km} - the effect of the interaction of the kth level of factor P with the mth level of factor D

AD_{lm} - the effect of the interaction of the lth level of factor A with the mth level of factor D

TSP_{ijk} - the effect of the interaction of the ith level of factor T with the jth level of factor S and the kth level of factor P

TSA_{ijl} - the effect of the interaction of the ith level of factor T with the jth level of factor S and the lth level of factor A

TSD_{ijm} - the effect of the interaction of the ith level of factor T with the jth level of factor S and the mth level of factor D

TPA_{ikl} - the effect of the interaction of the ith level of factor T with the kth level of factor P and the lth level of factor A

TPD_{ikm} - the effect of the interaction of the ith level of factor T with the kth level of factor P and the mth level of factor D

TAD_{ilm} - the effect of the interaction of the ith level of factor T with the lth level of factor A and the mth level of factor D

SPA_{jkl} - the effect of the interaction of the jth level of factor S with the kth level of factor P and the lth level of factor A

SPD_{jkm} - the effect of the interaction of the jth level of factor S with the kth level of factor P and the mth level of factor D

SAD_{jlm} - the effect of the interaction of the jth level of factor S with the lth level of factor A and the mth level of factor D

PAD_{klm} - the effect of the interaction of the kth level of factor P with the lth level of factor A and the mth level of factor D

$SPAD_{jklm}$ - the effect of the interaction of the jth level of factor S with the kth level of factor P, the lth level of factor A and the mth level of factor D

$TSPA_{ijkl}$ - the effect of the interaction of the ith level of factor T with the jth level of factor S, the kth level of factor P and the lth level of factor A

$TSPD_{ijkm}$ - the effect of the interaction of the ith level of factor T with the jth level of factor S, the kth level of factor P and the mth level of factor D

$TSAD_{ijlm}$ - the effect of the interaction of the ith level of factor T with the jth level of factor S, the lth level of factor A and the mth level of factor D

$TSPAD_{ijklm}$ - the effect of the interaction of the ith level of factor T with the jth level of factor S, the kth level of factor P, the lth level of factor A and the mth level of factor D

$\varepsilon_{(ijklm)n}$ - the random effect of the nth experimental unit in the ijklmth treatment combination

For the analysis of variance SPSS (Statistical Package for the Social Sciences) was used.

Table 3. 3. Sources of variance and degrees of freedom in determining the soil characteristics.

Sources of variance	Degrees of freedom
Soil type (S)	1
Provenance (P)	1
Acid rain (A)	1
Drought (D)	1
SP	1
SA	1
SD	1
PA	1
PD	1
AD	1
SPA	1
SPD	1
SAD	1
PAD	1
SPAD	1
Exp. error	16
Corrected total	31
Mean	1
Total	32

Table 3. 4. Sources of variance and degrees of freedom in determining the transpiration rate and the diffusive resistance.

Sources of variance	Degrees of freedom
Time (T)	5
Soil type (S)	1
Provenance (P)	1
Acid rain (A)	1
Drought (D)	1
TS	5
TP	5
TA	5
TD	5
SP	1
SA	1
SD	1
PA	1
PD	1
AD	1
TSP	5
TSA	5
TSD	5
TPA	5
TPD	5
TAD	5
SPA	1
SPD	1
SAD	1
PAD	1
SPAD	1
TSPD	5
TSAD	5
TSPA	5
TPAD	5
TSPAD	5
Exp. error	202
Corrected total	297
Mean	1
Total	298

Table 3. 5. Sources of variance and degrees of freedom in determining the chlorophyll fluorescence parameters.

Sources of variance	Degrees of freedom
Time (T)	2
Soil type (S)	1
Provenance (P)	1
Acid rain (A)	1
Drought (D)	1
TS	2
TP	2
TA	2
TD	2
SP	1
SA	1
SD	1
PA	1
PD	1
AD	1
TSP	2
TSA	2
TSD	2
TPA	2
TPD	2
TAD	2
SPA	1
SPD	1
SAD	1
PAD	1
SPAD	1
TSPA	2
TSPD	2
TSAD	2
TPAD	2
TSPAD	2
Exp. error	244
Corrected total	291
Mean	1
Total	292

4. RESULTS

4. 1. SOIL CHARACTERISTICS

4. 1. 1. Soil texture. Initially the heavy soil contained 60.23% sand, 37.00% clay and 2.77% silt, and the light soil 78.64% sand, 15.00% clay and 6.36% silt. After the 11-week treatment period, there were no major changes in the amounts of sand, clay, and silt that would lead to changes in soil texture. However, there was a slight decrease in the amount of clay. There was more clay in the pots supporting plants from the northern provenances of both pine and poplar (Table 4.1 and Appendix I, Table I). The small changes in the amounts of clay are probably due to the disturbance in the watering procedure before the treatment period. At this time some of the pots dried too much and upon rewatering some soil was lost. Resulting holes were filled with new soil. This changed percent of clay slightly.

4. 1. 2. Soil organic matter. Before the treatments both soils were medium to high humic; the heavy soil contained 4% organic matter, and the light soil, 6%. Acid rain caused a decrease in total organic matter in both soils and under both tree species (Table 4. 2 and Appendix I, Table II). Drought or provenance did not affect total organic matter. The two stress factors, acid rain and drought, did not change the amounts of

Table 4.1. Contents of sand, clay, and silt (%) in the heavy and light soils at the end of the experiment.

Provenance	Fractions	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
		drought	control	drought	control	drought	control	drought	control
					poplar				
Northern	sand	60.06	59.78	60.15	59.78	76.79	75.55	76.10	74.99
	silt	2.94	3.22	3.10	3.10	7.09	7.95	7.15	8.51
	clay	37.00	37.00	36.75	37.12	16.12	16.50	16.75	16.50
Southern	sand	60.85	59.77	60.78	59.78	75.85	76.53	75.59	75.56
	silt	5.10	3.10	2.90	2.10	8.02	7.72	7.53	7.94
	clay	34.05	37.13	36.32	38.12	16.13	15.75	16.88	16.50
					pine				
Northern	sand	59.73	59.28	60.15	59.88	76.28	75.68	75.10	76.11
	silt	3.24	3.23	3.10	3.00	7.09	8.20	7.65	8.01
	clay	37.03	37.49	36.75	37.12	16.63	16.12	17.25	15.88
Southern	sand	59.67	60.45	61.22	59.67	76.99	75.15	76.29	75.84
	silt	5.60	3.60	2.45	4.21	6.59	8.72	7.59	7.78
	clay	34.73	35.95	36.33	36.12	16.62	16.13	16.12	16.38

Table 4. 2. Total organic matter (%) in the heavy and light soils at the end of the experiment.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
				poplar				
Northern	4	3	4	5	3	4	4	5
Southern	3	3	4	5	3	3	5	6
				pine				
Northern	3	3	5	6	3	3	5	5
Southern	4	4	5	5	3	4	5	6

carbon and hydrogen in either soil (Table 4. 3 and Appendix I, Table III). However, provenance and its interaction with drought were significant for both tree species. Compared to controls, there was a slight decrease in the amount of carbon under plants from the northern provenances and a very slight increase in the amount of hydrogen, under plants from the southern provenances. As a result of the application of acid rain the amount of nitrogen in both soils and under both tree species slightly increased relative to controls. The interaction of acid rain with drought was also significant. However, the increase in soil nitrogen in pots that experienced the combined influence of both stress factors was smaller compared to the increase due to acid rain alone (Table 4. 3 and Appendix I, Table III).

The application of acid rain also caused a significant decrease in the C : N ratio compared to controls, indicating an accelerated decomposition rate (Table 4. 3 and Appendix I, Table III).

4. 1. 3. Soil pH. The changes in soil pH followed the same pattern wheather measured in water or in 0.01M $CaCl_2$. Initially the heavy soil had a pH of 7.50 in water and 7.20 in $CaCl_2$. The light soil was slightly acidic with pH 6.35 in water and 5.30 in $CaCl_2$ (Table 4. 4). The application of acid rain caused a significant pH decrease in both soils and under both tree species. The decrease in pH was greater under the northern provenances of both tree species and in the light soil. This resulted in a significant interaction of acid rain with provenance and soil type. Drought had no effect upon pH (Appendix I, Table IV).

Table 4. 3. Contents of carbon, hydrogen, and nitrogen (%) and the C : N ratio in the heavy and light soils at the end of the experiment.

Provenance	Elements	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
		drought	control	drought	control	drought	control	drought	control
					poplar				
Northern	carbon	1.09	1.12	0.93	0.98	0.57	0.78	0.58	0.98
	hydrogen	0.25	0.23	0.24	0.20	0.18	0.24	0.20	0.25
	nitrogen	0.015	0.015	0.01	0.01	0.035	0.04	0.025	0.04
	C : N	73	75	93	98	16	20	23	24
Southern	carbon	0.97	0.95	0.94	1.00	0.69	0.50	0.63	0.81
	hydrogen	0.20	0.18	0.23	0.19	0.21	0.23	0.23	0.22
	nitrogen	0.015	0.015	0.015	0.01	0.035	0.035	0.015	0.03
	C : N	65	63	63	100	20	14	42	27
					pine				
Northern	carbon	0.90	0.95	0.89	1.05	0.99	0.69	0.69	0.88
	hydrogen	0.22	0.28	0.21	0.20	0.31	0.26	0.30	0.23
	nitrogen	0.02	0.015	0.01	0.02	0.06	0.035	0.03	0.03
	C : N	45	63	89	52	16	20	23	29
Southern	carbon	0.97	1.02	0.95	1.02	0.94	1.14	0.87	1.04
	hydrogen	0.23	0.27	0.22	0.25	0.28	0.28	0.35	0.28
	nitrogen	0.01	0.02	0.01	0.015	0.04	0.06	0.04	0.04
	C : N	97	51	95	68	23	19	22	26

Table 4. 4. Soil pH in water and in 0.01M CaCl2 solution in the heavy and light soils at the end of the experiment.

Provenance	Solution	Heavy soil pH 3.0 drought	Heavy soil pH 3.0 control	Heavy soil pH 5.0 drought	Heavy soil pH 5.0 control	Light soil pH 3.0 drought	Light soil pH 3.0 control	Light soil pH 5.0 drought	Light soil pH 5.0 control
						__poplar__			
Northern	H2O	7.28	7.18	7.37	7.45	5.50	5.80	6.28	6.30
	CaCl2	7.00	6.97	7.17	7.20	5.17	5.00	5.27	5.30
Southern	H2O	7.45	7.28	7.47	7.47	6.00	5.90	6.28	6.28
	CaCl2	7.10	7.07	7.17	7.17	5.08	5.05	5.28	5.30
						__pine__			
Northern	H2O	7.35	7.27	7.40	7.45	5.77	5.60	6.17	6.30
	CaCl2	7.20	7.00	7.17	7.20	5.18	5.00	5.27	5.30
Southern	H2O	7.40	7.27	7.47	7.47	5.80	5.70	6.17	6.27
	CaCl2	7.10	7.07	7.17	7.17	5.25	5.05	5.27	5.30

4. 1. 4. Cation exchange capacity, percentage base saturation and amount of exchangeable ions. Initially both soils had almost the same cation exchange capacity (12meq/100 g soil for the heavy soil and 14 meq/100 g soil for the light one), but the heavy soil had higher percentage base saturation (71% compared to 57% for the light soil). Acid rain caused a significant decrease in the cation exchange capacity and percentage base saturation in both soils and under both tree species (Table 4. 5 and 4. 6, and Appendix I, Table V and VI). The other stress factor, drought, did not affect these chemical properties; neither did provenance.

Before the treatments the heavy soil contained less Al, and more Ca and Mg than the light soil, and approximately the same amount of K as the light soil (see 3. 1. 1). Despite the different properties of the two soil types, the stress factors caused similar changes in the amounts of exchangeable ions in both soils (Table 4. 7).

Exchangeable $Al^{\cdots}$ increased relative to controls (Table 4. 7). When the soils were supporting poplar the only significant changes were related to the interaction of acid rain with drought (Appendix I, Table VII). When the soils were supporting pine, exchangeable $Al^{\cdots}$ also increased when acid rain and drought were applied separately. The interaction of acid rain with drought had the strongest effect and in soils that experienced the combined influence of both stress factors the increase in levels of exchangeable $Al^{\cdots}$ was the greatest. As a whole exchangeable $Al^{\cdots}$ increased more in pots supporting seedlings from the southern provenance (Table 4. 7 and Appendix I, Table VII). These changes are an indication that drought is very

Table 4. 5. Mean total cation exchange capacity (meq/100g soil) for the heavy and light soils at the end of the experiment.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
				poplar				
Northern	8	9	11	13	12	11	14	15
Southern	9	8	12	11	12	11	14	14
				pine				
Northern	9	9	11	12	12	11	14	14
Southern	9	9	12	12	12	11	14	15

Table 4. 6. Mean base saturation (%) for the heavy and light soils at the end of the experiment.

Provenance	Heavy soil pH 3.0 drought	Heavy soil pH 3.0 control	Heavy soil pH 5.0 drought	Heavy soil pH 5.0 control	Light soil pH 3.0 drought	Light soil pH 3.0 control	Light soil pH 5.0 drought	Light soil pH 5.0 control
				poplar				
Northern	50	44.5	73	69	42	36	57	60
Southern	44	50	66.5	73	50	36.5	64	64
				pine				
Northern	55	44.5	64	66.5	41.5	36	57	64
Southern	55	44	66.5	67	42	36.5	64	60

Table 4. 7. Amount of exchangeable ions (ppm) in the heavy and light soils at the end of the experiment.

Provenance	Ions	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
		drought	control	drought	control	drought	control	drought	control
						poplar			
	$Al^{\cdot\cdot\cdot}$	0.3866	0.4261	0.4886	0.3563	2.210	1.743	2.202	1.853
Northern	$Ca^{\cdot\cdot}$	355.65	315.65	377.50	376.50	58.67	71.35	71.78	70.00
	$K^{\cdot}$	5.13	5.25	10.00	11.36	6.61	7.27	13.19	16.28
	$Mg^{\cdot\cdot}$	34.35	30.78	39.26	38.89	10.10	12.32	14.18	18.77
	$Al^{\cdot\cdot\cdot}$	0.3930	0.3995	0.4935	0.3157	1.830	2.421	2.263	1.873
Southern	$Ca^{\cdot\cdot}$	347.30	338.30	364.98	363.25	62.00	59.44	69.38	78.00
	$K^{\cdot}$	6.44	4.76	10.88	11.22	5.61	5.61	10.32	15.04
	$Mg^{\cdot\cdot}$	36.60	29.35	38.80	39.27	9.87	9.87	17.15	17.16
						pine			
	$Al^{\cdot\cdot\cdot}$	0.6088	0.3471	0.4949	0.3084	5.439	4.453	3.109	1.860
Northern	$Ca^{\cdot\cdot}$	335.95	330.80	361.15	381.30	63.22	64.64	70.97	72.16
	$K^{\cdot}$	7.00	5.19	10.64	11.98	7.12	4.72	12.17	15.15
	$Mg^{\cdot\cdot}$	35.32	32.45	36.91	40.93	10.45	8.28	13.95	16.22
	$Al^{\cdot\cdot\cdot}$	0.5263	0.5400	0.6212	0.3282	4.331	4.980	4.938	1.853
Southern	$Ca^{\cdot\cdot}$	343.30	315.35	355.00	371.15	69.36	59.84	67.80	68.45
	$K^{\cdot}$	5.69	5.02	11.91	12.65	7.02	5.13	14.69	15.89
	$Mg^{\cdot\cdot}$	40.13	31.50	38.93	40.02	12.79	9.11	14.78	16.70

important in the acidification process and enhances the adverse effect of acid rain. The requirements of the different species which are related to the uptake of nutrients are also important and can contribute to the changes due to acidifcation.

In pots treated with acid rain the amounts of exchangeable $Ca^{\cdot\cdot}$ decreased; other effects were nonsignificant (Table 4. 7 and Appendix I, Table VII). Exchangeable $Mg^{\cdot\cdot}$ and $K^{\cdot}$ in both soils decreased not only after acid rain was applied, but also as a result of drought. The combined influence of acid rain and drought caused significant decrease in the amounts of exchangeable $Mg^{\cdot\cdot}$ and $K^{\cdot}$ (Table 4. 7 and Appendix I, Table VII).

4. 2. PLANT CHARACTERISTICS

4. 2. 1. Pine

4. 2. 1. 1. Height and root collar diameter. Seedlings in the light soil were taller than seedlings in the heavy soil (Fig. 4. 1). In the heavy soil, seedlings from the northern provenance grew more than seedlings from the southern provenance, while in the light soil seedlings from the southern provenance were larger than seedlings from the northern provenance. Soil type was the most significant factor affecting height growth. The provenance difference was small and during the treatment period was gradually overshadowed by the effects of the soil type and the treatments (Appendix I, Table VIII). In both soils, seedlings treated with acid rain were

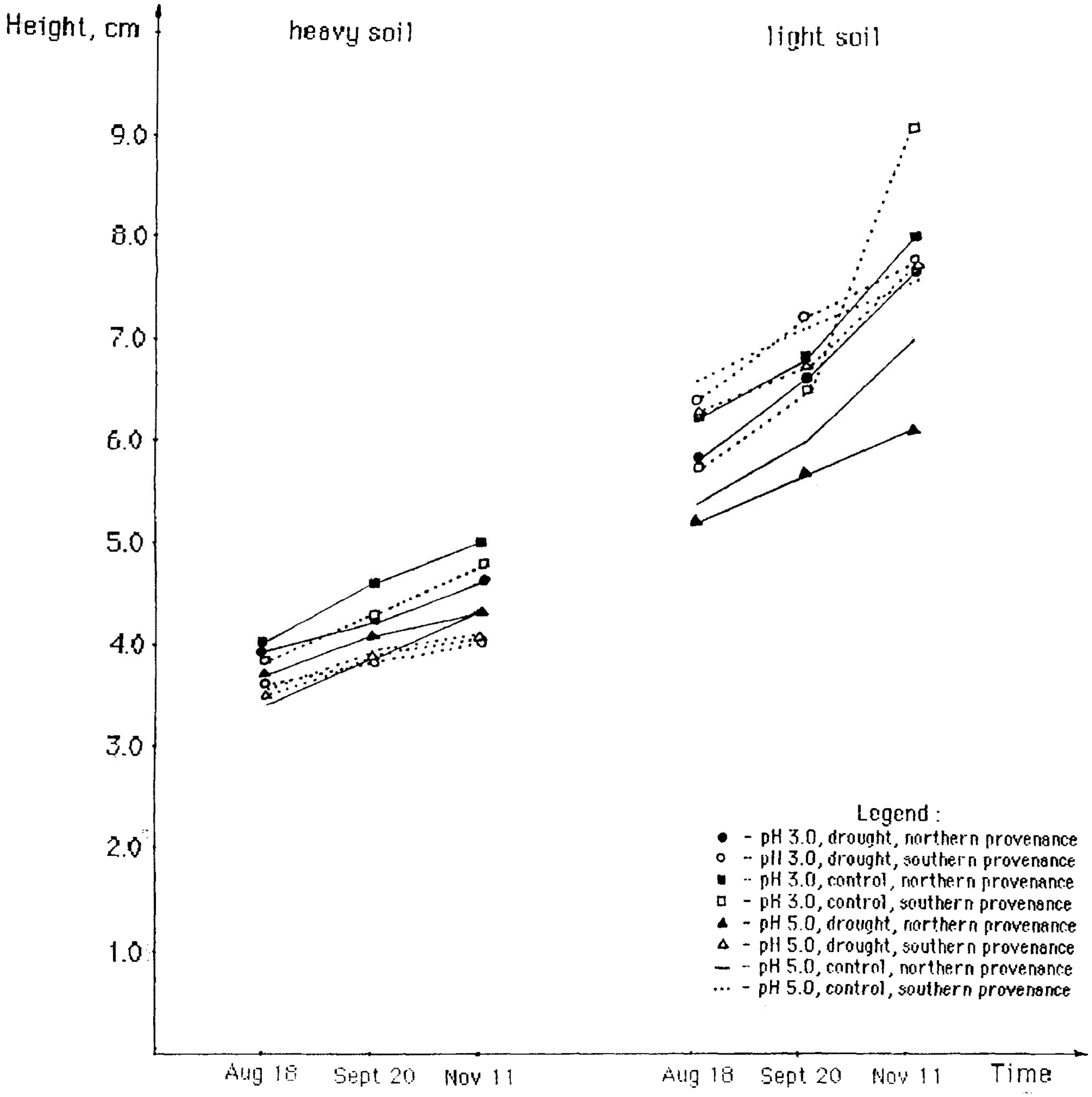

Fig. 4. 1. Changes in pine height during the treatment period.

tallest at the end of the treatment period. Even seedlings that experienced the effects of both acid rain and drought were taller than controls. In the heavy soil seedlings subjected to drought did not differ in height from controls, but in the light soil controls were taller, the difference being larger for seedlings from the northern provenance. During the treatment period the significance of both stress factors increased, but acid rain always had a stronger influence than drought. When combined, acid rain reduced the adverse effect of drought. Therefore, seedlings that experienced the influence of acid rain and drought were normally taller than seedlings subjected to drought.

At the end of the treatment period, seedlings in the light soil had larger root collar diameters than seedlings in the heavy soil (Table 4. 8 and Appendix I, Table IX). Drought had stronger effect than acid rain. In both soils, seedlings subjected to drought had the smallest root collar diameters and seedlings watered with acid rain, the largest. There was no interaction of the two stress factors. Although provenance was not a significant factor affecting diameter growth, its interactions with soil type, drought and acid rain were significant (Appendix I, Table IX). In the heavy soil, seedlings from the northern provenance had greater root collar diameters than seedlings from the southern provenance, and in the light soil, seedlings from the southern provenance were "thicker" than seedlings from the northern provenance. In both soils, drought reduced the root collar diameter in seedlings from the southern provenance more than in seedlings from the northern provenance.

Table 4. 8. Pine mean root collar diameter, mm.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	0.70	0.89	0.63	0.76	1.32	1.42	1.12	1.22
Southern	0.60	0.81	0.56	0.71	1.25	1.53	1.18	1.51

4. 2. 1. 2. Plot volume index of Marx. According to this parameter which is an expression of the overall performance, seedlings in the light soil performed better than seedlings in the heavy soil and this difference was highly significant (Table 4. 9 and Appendix I, Table X). Although provenance was also a significant factor, the treatments had a stronger effect. Seedlings watered with acid rain performed better than seedlings in the other treatments. Seedlings subjected to drought had the lowest PVI. The interactions of acid rain with provenance and soil type were both important. In the heavy soil seedlings from the northern provenance performed better, and in the light soil, the ones from the southern provenance.

4. 2. 1. 3. Dry weight. Seedlings in the light soil' produced more biomass, both aboveground and belowground, than seedlings in the heavy soil (Table 4. 10 and Appendix I, Table XI). Acid rain stimulated the production of aboveground biomass, but not of belowground biomass. In both soils, seedlings watered with acid rain had the largest dry weights and seedlings subjected to drought, the smallest. In the heavy soil, seedlings from the northern provenance were "heavier", but in the light soil seedlings from the southern provenance produced more aboveground biomass. Although provenance and drought were significant factors as well, their influence was not as strong as the influence of the soil type or acid rain. The interaction of soil type with provenance was the strongest, but the interactions of acid rain with soil type and drought also were significant. Seedlings that experienced the combined influence of acid rain and drought produced more aboveground biomass than seedlings subjected to drought, but less than seedlings watered with acid rain.

Table 4. 9. Mean values for the plot volume index of pine.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	17.81	24.30	16.00	18.58	54.05	61.09	38.32	38.32
Southern	12.18	21.37	13.07	16.15	54.02	65.85	50.75	64.22

Table 4. 10. Pine mean dry weight, g.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
	aboveground dry weight							
Northern	0.46	0.55	0.20	0.38	1.57	1.58	0.87	0.89
Southern	0.23	0.45	0.25	0.24	1.58	2.52	1.54	1.47
	belowground dry weight							
Northern	0.17	0.19	0.08	0.18	0.94	0.78	0.64	0.70
Southern	0.09	0.16	0.09	0.11	1.02	1.26	1.19	1.19

Root growth in the heavy soil was poor. Seedlings from both provenances and in all pots had dry weights under 0.2 g . The roots of seedlings from the northern provenance were heavier than the roots of seedlings from the southern provenance (Table 4. 10 and Appendix I, Table XI). In the light soil, root growth was much better than in the heavy soil. Seedlings from the southern provenance developed heavier root systems than seedlings from the northern provenance. This soil difference was probably due partly to the disturbances in the watering regime in pots of heavy soil at the beginning of the growing period (see 4. 1. 1). Although they occurred long before the treatments started and did not last long enough to visibly affect seedling growth and development, the drought stress may have affected root growth and development.

4. 2. 1. 4. Root surface area. Seedlings in the light soil developed much larger root surface area than seedlings in the heavy soil (Table 4. 11). The differences due to provenance were more strongly expressed in the light soil where seedlings from the southern provenance developed larger root surface areas than seedlings from the northern provenance. In the heavy soil, seedlings from the northern provenance had larger root surface areas than seedlings from the southern provenance. Soil type and provenance influenced the development of root surface area more strongly than did the stress factors (Appendix I, Table XII). Acid rain increased root surface area in the light soil, but not in the heavy one. Seedlings subjected

Table 4. 11. Pine mean root surface area, cm^2

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	34.50	35.55	18.65	38.17	284.12	286.15	212.97	216.88
Southern	18.80	33.43	18.80	23.52	316.05	388.28	285.67	363.68

to drought developed smaller root surface areas than well-watered seedlings. In both soils and for both provenances, seedlings watered with acid rain had the largest root surface areas and seedlings subjected to drought, the smallest. The interaction between the two stress factors did not affect the development of root surface area (Appendix I, Table XII).

4. 2. 1. 5. Shoot : root ratio. Seedlings in the heavy soil had larger shoot : root ratios than seedlings in the light soil (Table 4. 12). In both soils, seedlings watered with acid rain had the largest shoot : root ratios and controls, the smallest. Although drought alone was not a significant factor affecting the shoot : root ratio, its interaction with acid rain was significant (Appendix I, Table XIII). Seedlings that experienced the combined influence of acid rain and drought had larger shoot : root ratios than controls. These results can be considered as an indication that acid rain shifted the shoot : root ratio in favour of the shoots.

4. 2. 1. 6. Water saturation deficit. Water saturation deficit was measured at the beginning and at the end of a drought cycle. At the beginning of the drought cycle all seedlings in both soils had a water saturation deficit under 10%, but it was higher in seedlings that had already experienced drought (Fig. 4. 2). Effects of acid rain and its interaction with drought were also statistically significant (Appendix I, Table XIV).

Table 4. 12. Pine mean shoot : root ratio.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	2.79	3.06	2.25	2.19	1.73	2.03	1.31	1.28
Southern	2.46	2.81	2.95	2.40	1.65	2.25	1.25	1.20

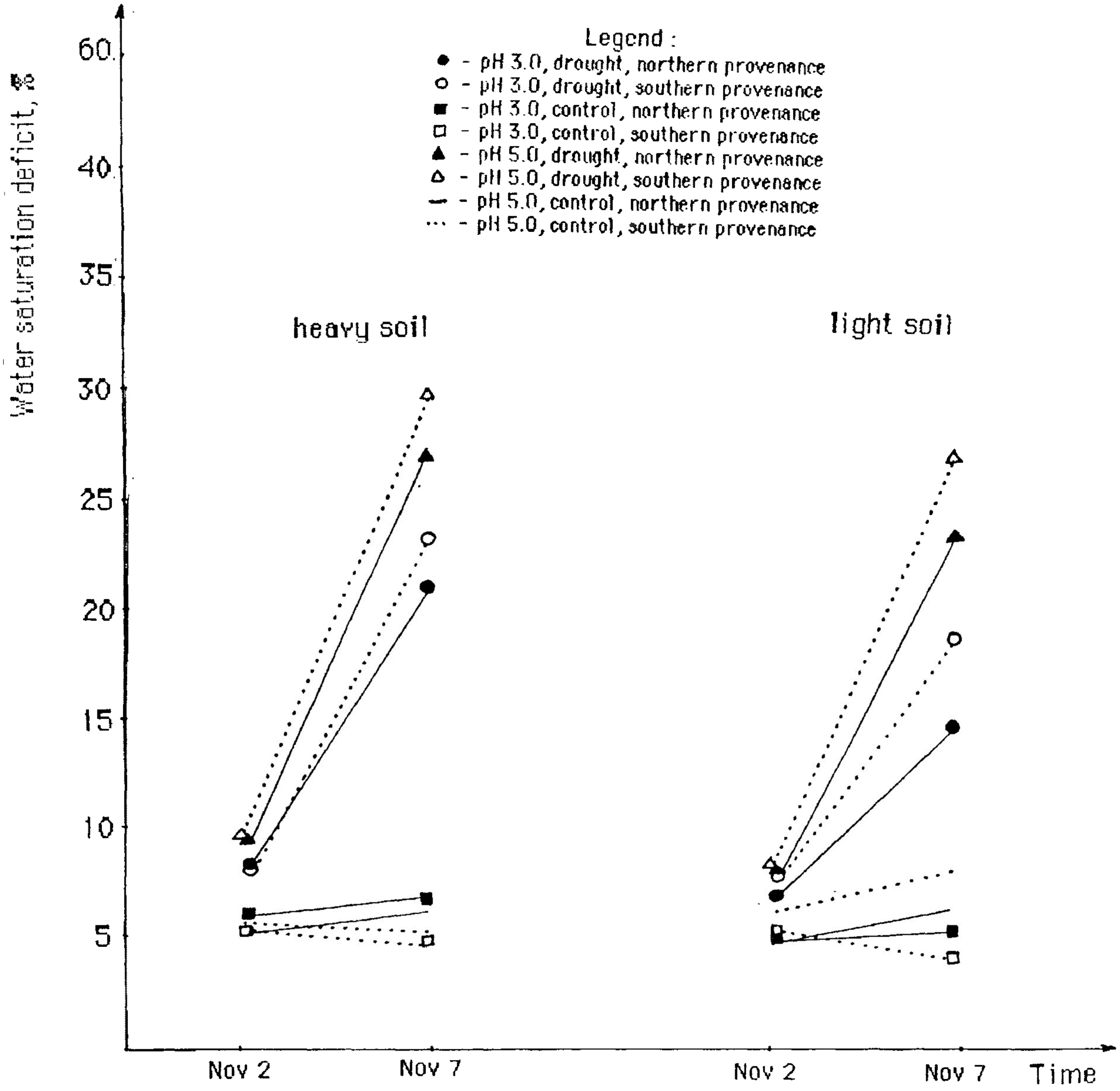

Fig. 4. 2. Development of water saturation deficit in pine seedlings during a drought cycle.

Seedlings subjected to both acid rain and drought had higher water saturation deficit than seedlings watered with acid rain only. Controls had the lowest water saturation deficit. Although at this time soil type did not significantly affect water saturation deficit, treatment differences were more distinct in the heavy soil.

By the end of the drought cycle, effects of drought, acid rain and their interaction increased markedly. At the end of the drought cycle, soil type and provenance also became significant (Appendix I, Table XIV). Seedlings in the heavy soil developed a little higher water saturation deficit than seedlings in the light soil. In both soils, seedlings from the southern provenance had higher water saturation deficit than seedlings from the northern provenance. Seedlings subjected to drought had the highest water saturation deficit. Seedlings previously watered with acid rain developed lower water saturation deficits than seedlings that received water with pH 5.0.

<u>4. 2. 1. 7. Fluorescence.</u> Variable fluorescence (Fv), the ratio between the variable and the maximum fluorescence (Fv/Fm), and the half-raise time necessary for the fluorescence to increase from 0 to the peak (1/2 t) were measured at the beginning, in the middle and at the end of a drought cycle.

Seedlings in the light soil had higher values of Fv and Fv/Fm than seedlings in the heavy soil (Table 4. 13). In both soils, both parameters decreased by the end of the measurement period; changes over time were highly significant (Appendix I, Table XV). Drought significantly affected fluorescence in pine. Seedlings subjected to drought had the lowest values

Table 4. 13. Mean values for Fv, Fv/Fm and the half-raise time for pine seedlings.

			Heavy soil				Light soil			
			pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Parameter	Day	drought	control	drought	control	drought	control	drought	control
Northern	Fv	4 Nov	0.41	0.55	0.34	0.51	0.56	0.51	0.57	0.61
	Fv/Fm	4 Nov	0.745	0.734	0.665	0.774	0.743	0.730	0.75	0.746
	1/2 t	4 Nov	145	165	116	143	163	172	156	135
	Fv	6 Nov	0.36	0.48	0.30	0.38	0.42	0.31	0.45	0.37
	Fv/Fm	6 Nov	0.741	0.762	0.728	0.738	0.748	0.779	0.789	0.786
	1/2 t	6 Nov	110	98	93	84	101	94	102	105
	Fv	8 Nov	0.13	0.25	0.13	0.14	0.19	0.31	0.18	0.17
	Fv/Fm	8 Nov	0.547	0.584	0.536	0.633	0.627	0.612	0.600	0.686
	1/2 t	8 Nov	100	100	61	115	131	107	85	131
Southern	Fv	4 Nov	0.47	0.51	0.46	0.52	0.54	0.64	0.65	0.58
	Fv/Fm	4 Nov	0.647	0.776	0.663	0.722	0.768	0.740	0.754	0.792
	1/2 t	4 Nov	160	138	165	146	142	163	152	149
	Fv	6 Nov	0.34	0.44	0.27	0.47	0.33	0.44	0.52	0.47
	Fv/Fm	6 Nov	0.716	0.780	0.763	0.736	0.789	0.800	0.809	0.749
	1/2 t	6 Nov	87	115	112	106	122	112	110	112
	Fv	8 Nov	0.17	0.23	0.18	0.21	0.17	0.22	0.18	0.21
	Fv/Fm	8 Nov	0.509	0.592	0.477	0.637	0.612	0.602	0.594	0.600
	1/2 t	8 Nov	78	82	62	103	114	108	86	124

of Fv and Fv/Fm. Acid rain and the combined influence of both stress factors caused significant decrease of Fv/Fm, but not of Fv.

The 1/2 t changed in a similar way. It was higher in seedlings in the light soil and decreased over time. Both drought and acid rain caused a significant decrease in 1/2 t, but the interaction between the two stress factors did not affect this parameter. Provenance was not a significant factor affecting fluorescence (Table 4. 13 and appendix I, Table XV).

4. 2. 2. Poplar

4. 2. 2. 1. Height and stem diameter. At the beginning of the treatment period, cuttings in the light soil were taller than cuttings in the heavy soil (Fig. 4. 3). At this time provenance most strongly influenced height growth, but with time the influence of the treatments increased markedly (Appendix I, Table XVI). However, at the end of the treatment period, in both soils cuttings from the southern provenance were taller than cuttings from the northern provenance; the difference was expressed more strongly in the heavy soil. Acid rain and drought also significantly affected height growth. Cuttings treated with acid rain were the tallest. The effect of drought was more clearly pronounced in the light soil, but in both soils cuttings that experienced drought were the smallest. These tendencies remained the same during the whole treatment period.

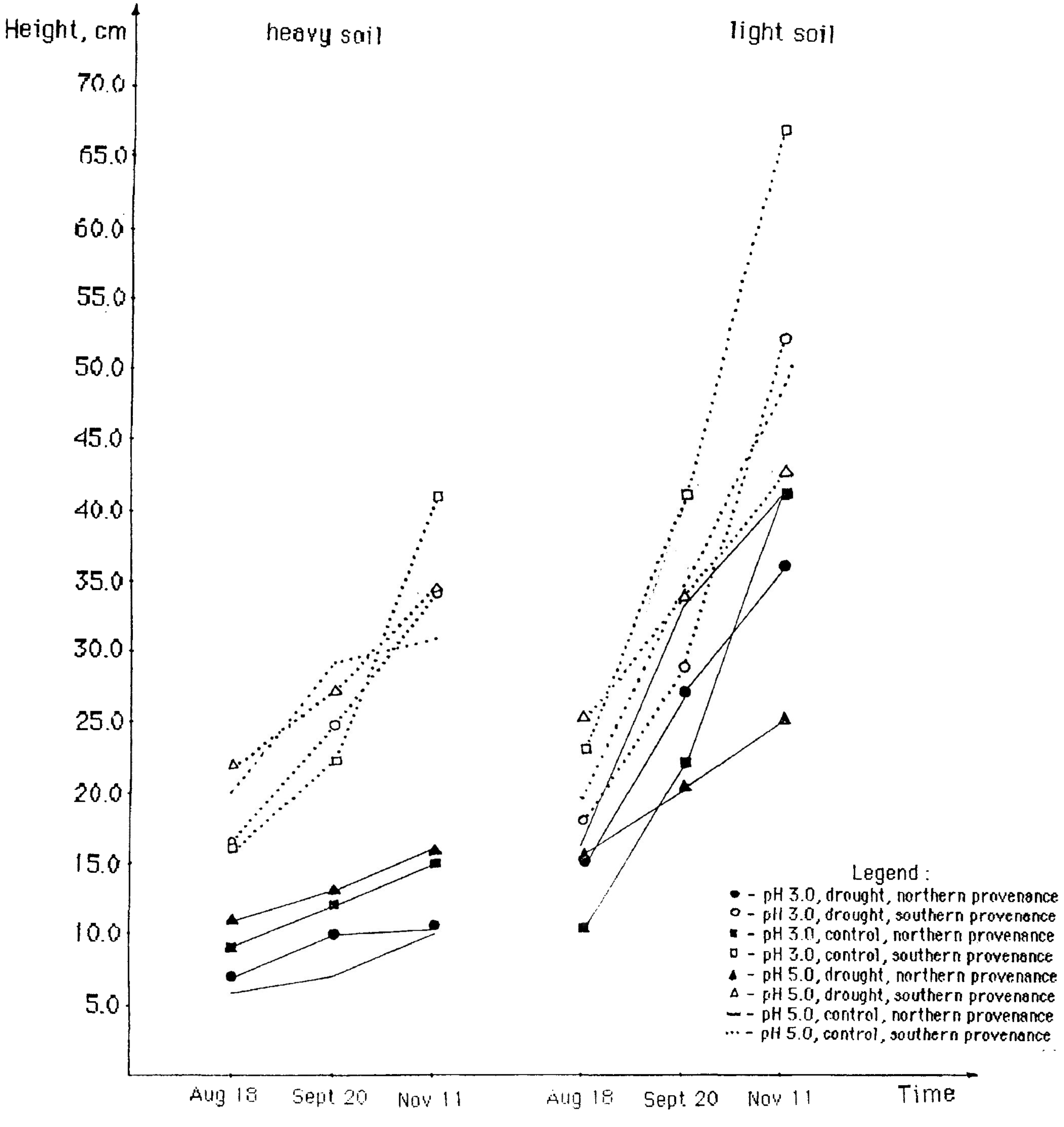

Fig. 4. 3. Changes in poplar height during the treatment period.

All cuttings in the light soil developed larger stem diameters than cuttings in the heavy soil (Table 4. 14). In both soils, cuttings from the southern provenance had larger stem diameters than cuttings from the northern provenance. Stem diameter growth was most strongly affected by soil type and provenance. Drought significantly affected diameter growth, but acid rain did not. However, the interactions of acid rain with drought, soil type and provenance were all significant (Appendix I, Table XVII). In both soils, cuttings subjected to drought had the smallest stem diameters. Although the differences were not statistically significant, cuttings watered with acid rain tended to have larger stem diameters than cuttings in the other treatments. Acid rain reduced the adverse effect of drought. Cuttings that experienced the combined influence of acid rain and drought had larger stem diameters than cuttings subjected to drought, but smaller diameters than cuttings watered with acid rain.

4. 2. 2. 2. Dry weight. Cuttings in the heavy soil had less dry weight, both aboveground and belowground, than cuttings in the light soil (Table 4. 15). In both soils, cuttings from the southern provenance produced more biomass than cuttings from the northern provenance, but the effect of provenance was significant only for the production of aboveground biomass (Appendix I, Table XVIII). In both soils, cuttings subjected to drought had the smallest dry weights and cuttings watered with acid rain, the largest. Drought had a stronger effect than acid rain. Interactions of acid rain with drought, soil type or provenance were nonsignificant. Acid rain and its interaction with soil type were significant for the production of belowground biomass. Cuttings watered with acid rain had less belowground

Table 4. 14. Poplar mean stem diameter, cm.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	2.18	2.99	2.20	2.26	3.82	5.94	3.80	5.28
Southern	3.27	3.79	3.17	3.84	4.30	5.34	4.75	5.17

Table 4. 15. Poplar mean dry weight, g.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
	aboveground dry weight							
Northern	1.00	1.92	0.87	1.04	3.38	6.01	2.66	5.22
Southern	2.21	3.77	1.46	2.50	3.95	7.48	4.33	5.77
	belowground dry weight							
Northern	0.83	1.21	1.11	1.71	2.14	3.40	2.71	4.52
Southern	1.19	1.52	1.40	2.21	1.55	2.38	3.16	3.54

biomass than controls, but more than cuttings subjected to drought. Although drought alone caused a significant decrease in the production of belowground biomass, its interactions with acid rain, soil type and provenance were not statistically significant.

4. 2. 2. 3. Root surface area. All cuttings in the light soil had larger root surface areas than cuttings in the heavy soil (Table 4. 16). In the heavy soil, cuttings from the southern provenance had larger root surface areas than cuttings from the northern provenance, and in the light soil cuttings from the northern provenance had larger root surface areas than cuttings from the southern provenance. Effects of acid rain and drought were both significant, but their interaction was not (Appendix I, Table XIX). Although not the heaviest, control cuttings in both soils had the largest root surface areas. In the heavy soil, they were followed by cuttings watered with acid rain, but in the light soil by cuttings subjected to drought.

4. 2. 2. 4. Shoot : root ratio. Cuttings in the light soil had larger shoot : root ratios. In both soils, cuttings from the southern provenance had larger shoot : root ratios. Also in both soils, cuttings watered with acid rain had the largest shoot : root ratios and cuttings subjected to drought, the smallest. Although effects of soil type and provenance were significant for the shoot : root ratio, acid rain had the strongest influence on this parameter, and drought, the weakest. The interaction of acid rain with soil type was also significant (Table 4. 17 and Appendix I, Table XX). Cuttings watered with acid rain in the heavy soil had smaller shoot : root ratios than cuttings watered with acid rain in the light soil.

Table 4. 16. Poplar mean root surface area, cm^2.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	drought	control	drought	control	drought	control	drought	control
Northern	54.43	74.84	60.84	131.88	242.30	288.37	331.53	546.88
Southern	71.17	119.32	60.14	187.88	162.23	232.36	261.67	361.10

Table 4. 17. Poplar mean shoot : root ratio.

	Heavy soil				Light soil			
	pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenances	drought	control	drought	control	drought	control	drought	control
Northern	1.10	1.45	0.72	0.79	1.77	1.89	0.89	1.47
Southern	2.07	2.57	1.05	1.24	2.52	3.27	1.45	1.39

4. 2. 2. 5. Water saturation deficit. At the beginning of the drought cycle all cuttings had a water saturation deficit under 10% (Fig. 4. 4). At this time only drought had some influence, and cuttings that had already experienced drought had slightly higher water saturation deficit than cuttings in the other treatments. With the drying of the soil the influence of drought, acid rain and provenance increased (Appendix I, Table XXI). At the end of the drought cycle the water saturation deficit in cuttings subjected to drought increased to about 20%. Cuttings which were previously watered with acid rain had lower water saturation deficit than controls (receiving water with pH 5.0). Although cuttings from the northern provenance tended to develop a little higher water saturation deficit, the influence of the provenance was not strong.

4. 2. 2. 6. Transpiration and diffusive resistance. Transpiration and diffusive resistance were measured during a drought cycle at the beginning of the treatment period, in September, and at the end of the treatment period, in November.

At the beginning of the treatment period, in September, all cuttings had higher transpiration rates than at the end of the treatment period, in November (Fig. 4. 5 and 4. 6). Before the drought cycle cuttings in the light soil had higher transpiration rates than cuttings in the heavy soil (Fig. 4. 5). By the end of the drought cycle transpiration rates in all cuttings decreased, but remained higher in cuttings in the light soil. Cuttings that regularly received water or acid rain had almost the same transpiration

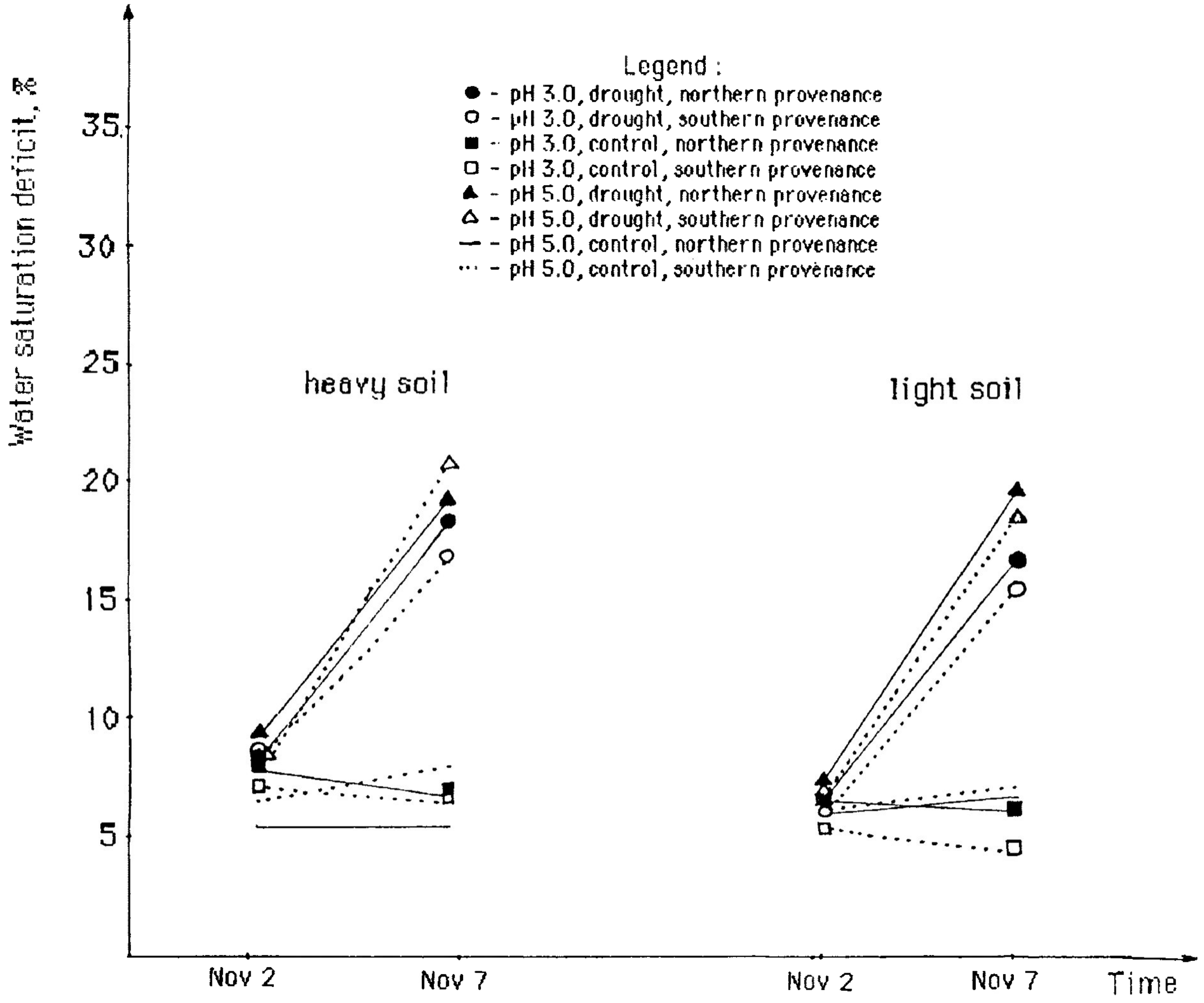

Fig. 4. 4. Development of water saturation deficit in poplar cuttings during a drought cycle.

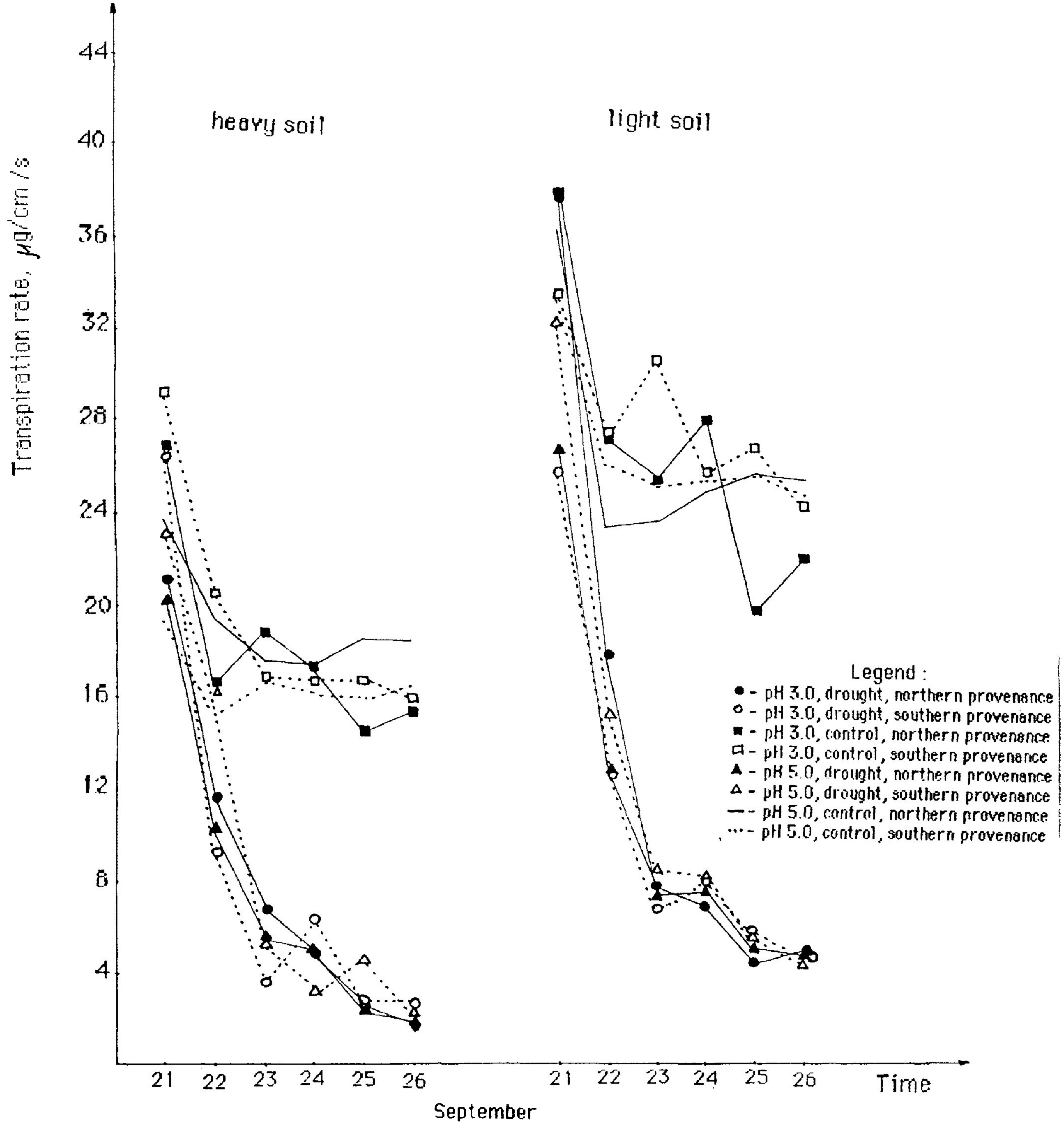

Fig. 4. 5. Changes in transpiration rates in poplar cuttings during a drought cycle at the begining of the treatment period.

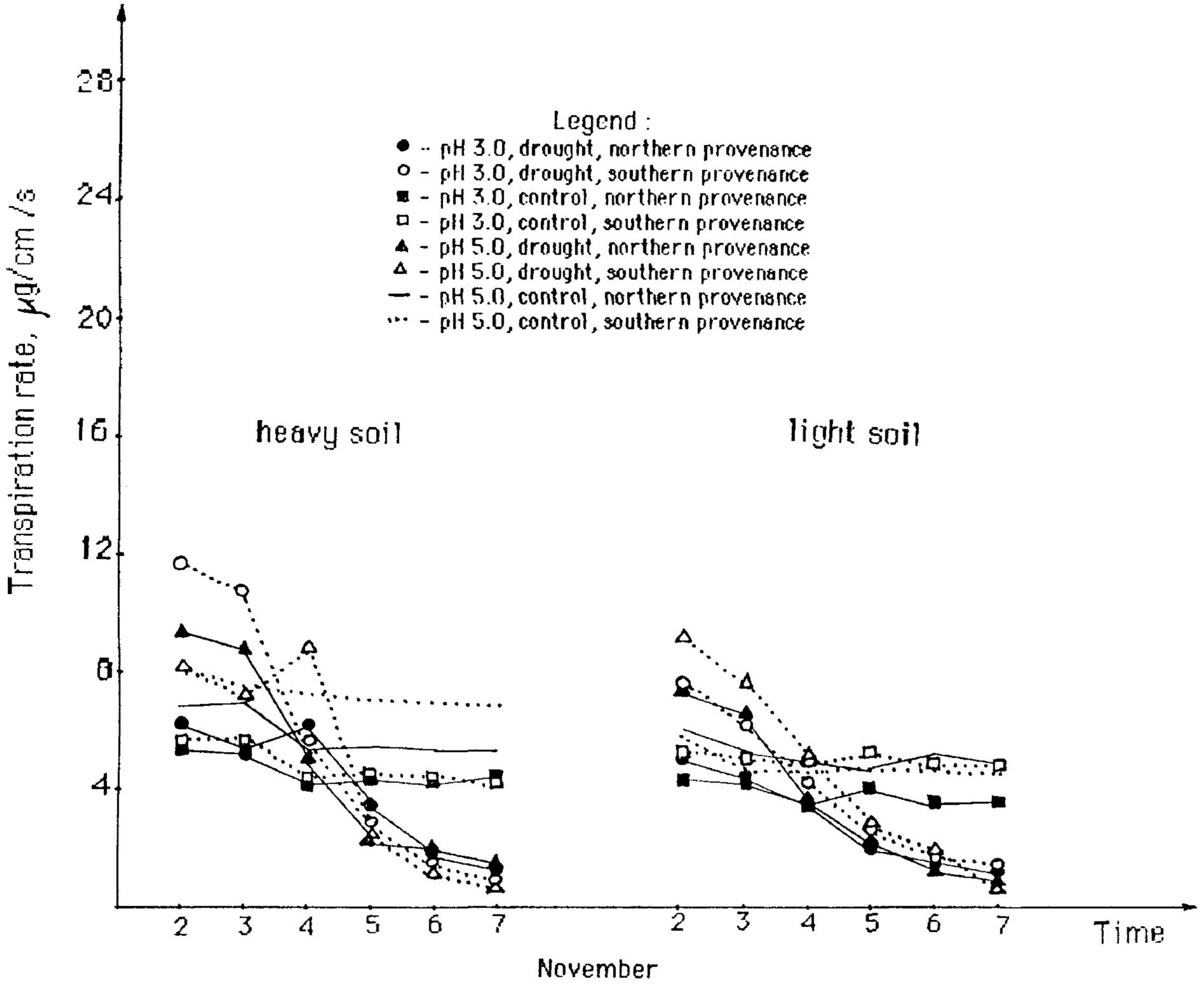

Fig. 4. 6. Changes in transpiration rates in poplar cuttings during a drought cycle at the end of the treatment period.

rates during the whole measurement period. Drought was the most significant factor affecting this physiological process (Appendix I, Table XXII). In cuttings subjected to drought, transpiration rates continued to decrease after Sept 23 and reached their minimal levels at the end of the measurement period, Sept 26. When watered with acid rain cuttings in both soils and from both provenances had as a whole lower transpiration rates than controls. This was more clearly expressed after Sept 24 for cuttings from the northern provenance and after Sept 25 for cuttings from the southern provenance. The interaction between the two stress factors, acid rain and drought, was also significant. At the end of the drought cycle, transpiration rates in cuttings that experienced the combined influence of acid rain and drought were slightly higher than in cuttings that received water with pH 5.0. The small differences between cuttings from the two provenances were not statistically significant.

In November, at the end of the treatment period, transpiration rates changed in the same way as in September (Fig. 4. 6). However, at this time the influence of drought decreased, but the influence of acid rain increased. The interaction between acid rain and drought was also significant (Appendix I, Table XXIII). Before the drought cycle cuttings in the heavy soil had a little higher transpiration rates than cuttings in the light soil, but by the end of the drought cycle transpiration rates in both soils reached almost the same levels in all cuttings. Cuttings that had not previously experienced drought cycles maintained almost the same transpiration rates during the whole measurement period. During the drought cycle transpiration rates decreased in cuttings subjected to drought and in cuttings that experienced the combined influence of acid rain and drought in both soils. However, when cuttings were previously watered with acid rain they had a little higher transpiration rates than controls. By the end of the treatment period provenance also became a significant factor affecting transpiration. In both soils, cuttings from the southern provenance had a little higher transpiration rates than cuttings from the northern provenance.

The diffusive resistance of the leaf tissues is closely related to transpiration. When transpiration increases, the diffusive resistance decreases and vise versa. The changes in diffusive resistance due to the treatments or the soil type corresponded to the changes in transpiration (Fig. 4. 7 and 4. 8). However, in September drought and soil type were more significant for diffusive resistance than for transpiration (Appendix I, Table XXII). In the heavy soil, all cuttings had a little higher diffusive resistance than cuttings in the light soil. Acid rain and its interaction with drought did not affect this parameter. By the end of the first measurement period, cuttings subjected to drought had higher diffusive resistance than cuttings in the other treatments.

At the end of the treatment period, in November, the effect of drought was still highly significant (Appendix I, Table XXIII). Acid rain and its interaction with drought also became significant. By the end of the drought cycle the diffusive resistance of cuttings subjected to drought and of cuttings that experienced the combined influence of acid rain and drought increased markedly in both soils. At this time soil type and provenance did not affect diffusive resistance.

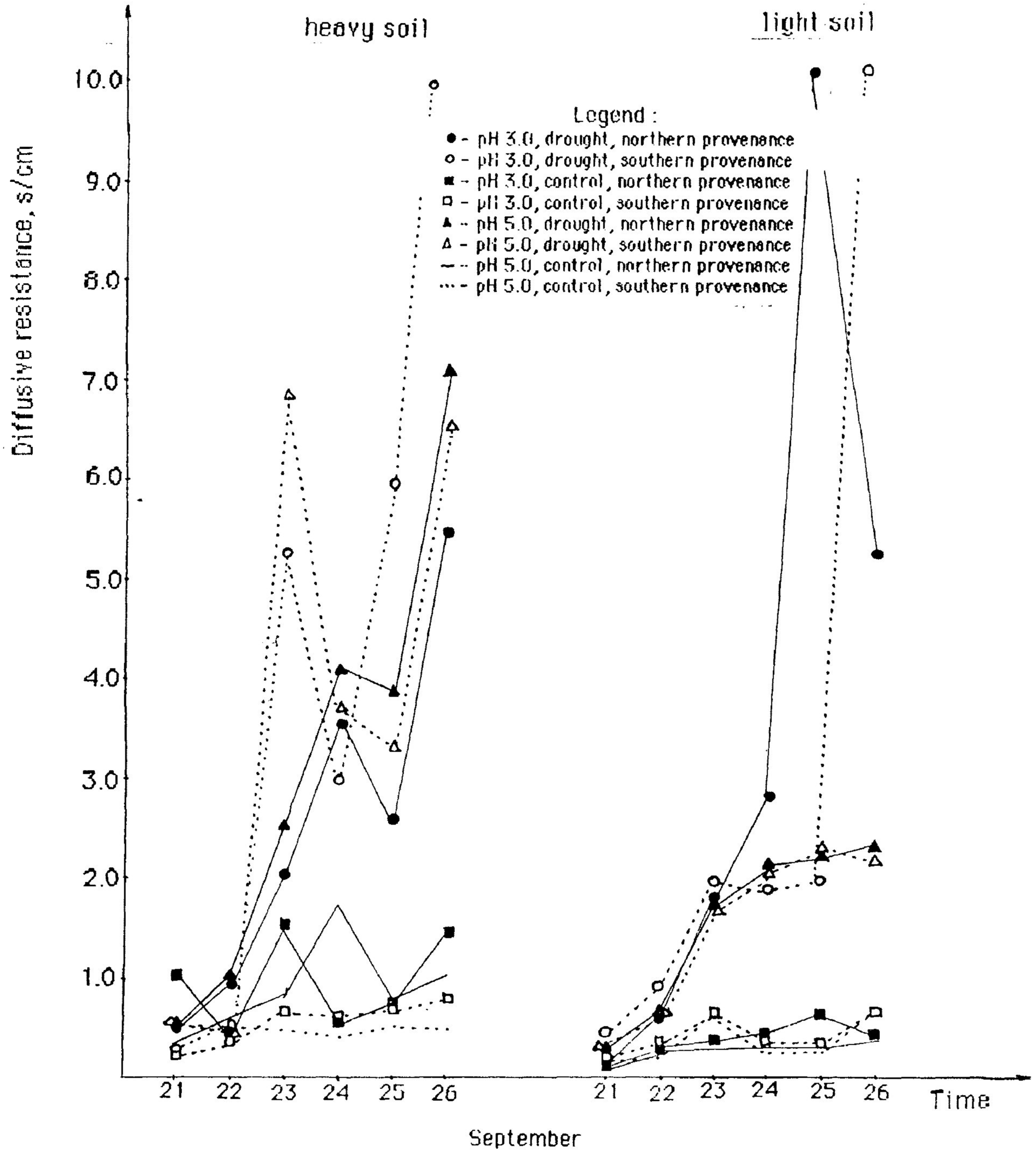

Fig. 4. 7. Changes in diffusive resistance in poplar cuttings during a drought cycle at the begining of the treatment period.

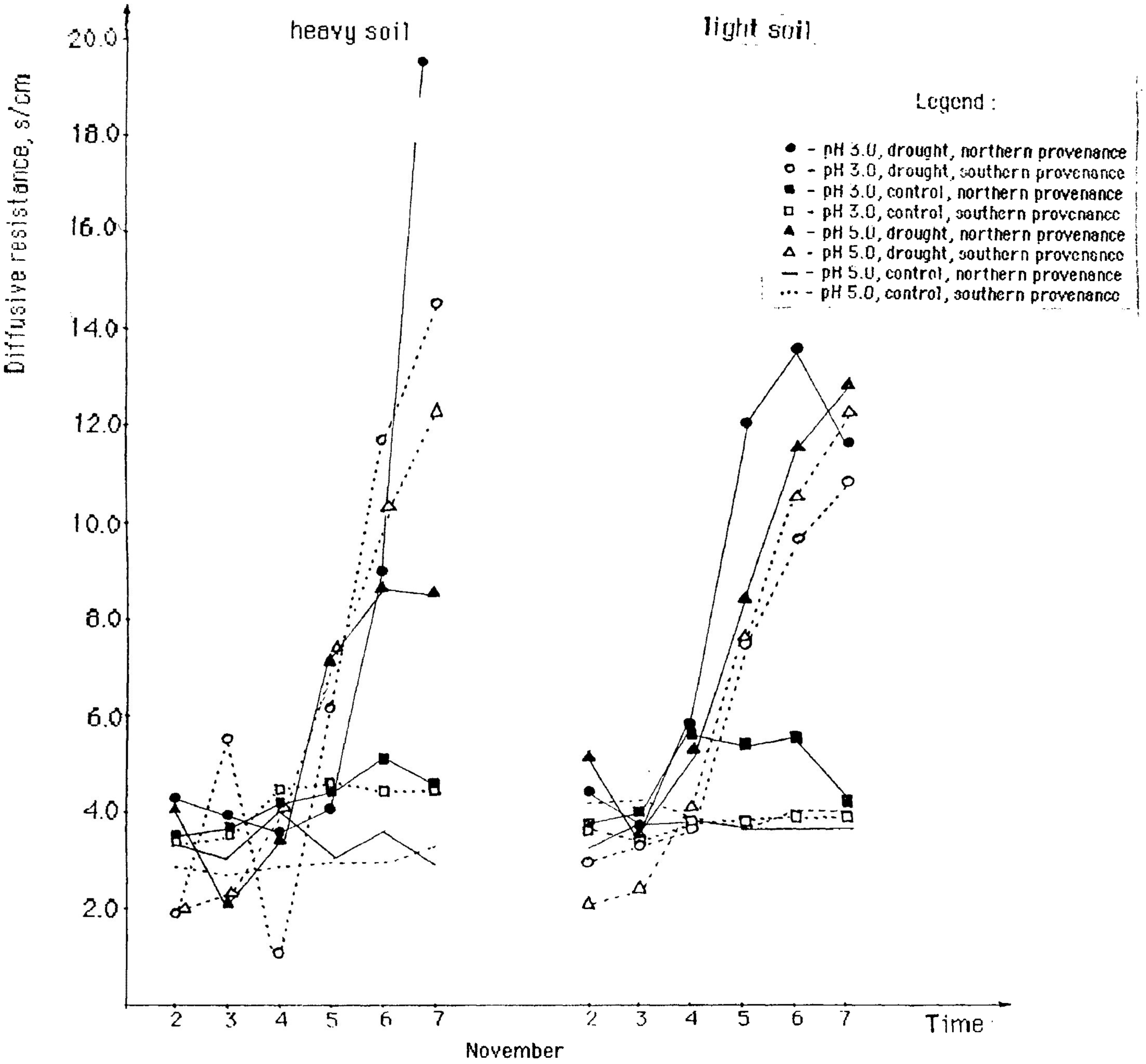

Fig. 4. 8. Changes in diffusive resistance in poplar cuttings during a drought cycle at the end of the treatment period.

4.2.2.7. Fluorescence. As in the case with pine, Fv, Fv/Fm and 1/2 t were measured during a drought cycle. Fv and Fv/Fm decreased during the drought cycle and these changes were statistically significant(Table 4. 18 and Appendix I, Table XXIV). Cuttings in the light soil had a little higher levels of Fv and Fv/Fm during the whole drought cycle. In both soils, cuttings from the southern provenance tended to have higher Fv and Fv/Fm, especially at the end of the measurement period. Drought affected Fv more strongly than it did Fv/Fm. Acid rain and the combined influence of both stress factors did not affect Fv and Fv/Fm. However, the interaction of soil type with acid rain affected significantly both Fv and Fv/Fm. Cuttings watered with acid rain had the highest levels of Fv and Fv/Fm compared to cuttings in the other treatments. Cuttings watered with acid rain in the light soil had higher Fv and Fv/Fm than cuttings watered with acid rain in the heavy soil.

The 1/2 t changed in a similar way. It decreased during the measurement period and these changes were statistically significant (Table 4. 18 and Appendix I, Table XXIV). The different properties of the two soils were not important for this parameter, but provenance was significant. In the heavy soil 1/2 t was higher in cuttings from the northern provenance, while in the light soil it tended to be higher in cuttings from the southern provenance. Acid rain and its interaction with soil type were also important. Cuttings watered with acid rain had the highest 1/2 t in the test. Moreover, the 1/2 t tended to be higher in cuttings in the heavy soil than in cuttings in the light soil. Drought was significant only when interacting with soil type. Cuttings subjected to drought in the heavy soil had higher 1/2 t than cuttings subjected to drought in the light soil.

Table 4. 18. Mean values for Fv, Fv/Fm and the half-raise time for poplar cuttings.

			Heavy soil				Light soil			
			pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Parameter	Day	drought	control	drought	control	drought	control	drought	control
Northern	Fv	4 Nov	0.53	0.69	0.59	0.59	0.65	0.73	0.72	0.86
	Fv/Fm	4 Nov	0.781	0.807	0.778	0.788	0.794	0.791	0.792	0.795
	1/2 t	4 Nov	163	127	154	127	134	159	130	136
	Fv	6 Nov	0.50	0.61	0.43	0.50	0.57	0.64	0.67	0.72
	Fv/Fm	6 Nov	0.783	0.813	0.801	0.793	0.778	0.802	0.790	0.801
	1/2 t	6 Nov	124	102	107	103	110	121	104	105
	Fv	8 Nov	0.30	0.39	0.28	0.30	0.28	0.35	0.26	0.36
	Fv/Fm	8 Nov	0.715	0.752	0.710	0.733	0.715	0.737	0.703	0.719
	1/2 t	8 Nov	110	115	106	100	95	112	60	98
Southern	Fv	4 Nov	0.80	0.83	0.72	0.75	0.67	0.79	0.78	0.83
	Fv/Fm	4 Nov	0.771	0.807	0.780	0.784	0.774	0.766	0.780	0.791
	1/2 t	4 Nov	138	122	149	134	138	159	135	155
	Fv	6 Nov	0.59	0.76	0.59	0.60	0.59	0.65	0.60	0.65
	Fv/Fm	6 Nov	0.807	0.814	0.822	0.806	0.773	0.796	0.785	0.810
	1/2 t	6 Nov	103	112	117	126	110	129	117	110
	Fv	8 Nov	0.32	0.40	0.30	0.33	0.37	0.44	0.35	0.38
	Fv/Fm	8 Nov	0.711	0.694	0.683	0.705	0.642	0.713	0.699	0.696
	1/2 t	8 Nov	103	110	97	103	105	110	96	115

5. DISCUSSION

5. 1. SOIL CHARACTERISTICS

The effects of acidic deposition involve complex processes which may interact in a manner such that the relatively small change in soil pH may be accompanied by very significant changes in soil chemistry. The responses of individual soil systems are highly variable, depending on the duration and intensity of deposition and the properties of the soil (Singh, 1985; Reuss and Johnson, 1986).

Even for the relatively short treatment period in our experiment, acid rain had significant effects on soil chemistry. The changes in our light soil showed that the mineralization of organic matter was enhanced and it became richer in available nitrogen. Although it has been reported that as a resultof the application of acid rain total nitrogen in the soil does not change (Cheong, 1987), our results support observations of increased total nitrogen after acid rain has been applied (Nihlgard, 1985; Schutt and Cowling, 1985; Haynes and Swift, 1986; Reuss and Johnson, 1986; McColl and Firestone, 1987). However, in some of these cases the proportions of NO_3 to NH_4 have also been altered (Haynes and Swift, 1986). As we have no detailed information about NO_3 and NH_4, it is impossible to speculate about which processes are prevailing in our soils. The fact that we simply added nitrogen to the soils by using nitric acid as a component of our acid rain and probably the complex plant soil interactions which are related to the uptake of nutrients, are also important (Haynes, 1986; Binkley *et al.*, 1989).

As expected from numerous reports in the literature (Singh,1985; MacDonald *et al.*, 1986; McFee *et al.*, 1986; Schultze, 1989; Cheong, 1987; McColl and Firestone, 1987; Binkley *et al.*, 1989, and others) acid rain caused a decrease in soil pH in both soils. This rapid decrease in soil pH and soil acidification were to some extent due also to the experimental design. It is well known that rapid acidification can be achieved with the direct use of acids, particularly when applied through irrigation water, as was our case (Malmer, 1976; Haynes and Swift, 1986). The greater decrease in pH in our light soil compared to the heavy soil was expected. This is because soils with high pH are normally more resistant to acidifying processes owing to their high calcium content which gives rise to a high buffering capacity. Acid soils, where hydrated aluminum compounds represent the most important buffer system, have a lower buffering capacity and are more easily acidified (Malmer, 1976).

The main reason for the decrease of the cation exchange capacity and the percentage base saturation, and for the changes in the amounts of exchangeable ions is rapid acidification (Cheong, 1987; Carlson and Ragsdale, 1988; Kim and Lee, 1988; Nygaard and Abrahamsen, 1991). Charge balance considerations dictate that the increased anion concentrations must be accompanied by an equivalent increase in cations in solution, and the nature of the soil chemical processes involved is such that this is accomplished by a shift in the relative proportions of the anions as well as an increase in the total concentration. This shift is in direction of an increase in the proportions of cations having higher valence at the expense of a decreased proportion of cations having lower valence, i.e. the increase in the concentration of H^{+} , due to acid rain, is accompanied by an increase in the concentration of Al^{+++} (Reuss and Johnson, 1986). The increase of exchangeable Al^{+++} with soil acidification reflects also the affinity that Al^{+++} species generally have for the cation exchange surfaces of soils and the ability of Al^{+++} to strongly complex with organic matter (Cammerer, 1983; Haynes and Swift, 1986). Solubilized Al^{+++} also increases as levels of exchangeable Al^{+++} increase (Haynes and Swift, 1986; Tomlinson *et al.*, 1990).

It is well known that soil acidification results in the build-up of soluble salts in soil solution and subsequent leaching of these salts is required to maintain a fertile environment (Malmer, 1976; Haynes and Swift, 1986). The decreases in levels of exchangeable Ca^{++} , Mg^{++} and K^{+} as soils were acidified were result of the replacement of cations on exchange sites by added H^{+}(Haynes and Swift, 1986). As Al^{+++} enters the soil solution at lower pH (less than 4.2), it becomes a predominant cation and together with H^{+} displaces the nutrient cations which later are gradually leached from the soil with an increasing rate (Cammerer, 1983; Baule, 1985; MacDonald *et al.*, 1986; Reuss and Johnson, 1986). Therefore decreasing base saturation and increasing leaching of Ca^{++} , Mg^{++} and K^{+} with increasing soil acidification would be reasonably predictable (Baule, 1985; MacDonald *et al.*, 1986; Haynes and Swift, 1986; Reuss and Johnson, 1986; Ulrich and Pankrath, 1983; Tomlinson *et al.*, 1990). Our light soil soil was slightly acidic and had lower base saturation before acid rain was applied. This can explain the greater decreases in levels of exchangeable Ca^{++} and Mg^{++} in this soil as acid rain was applied, because trivalent Al^{+++} , released in acidic soils, is more strongly absorbed on the exchange sites on soil particles than the lower-valence nutrient cations Ca^{++}, Mg^{++} and K^{+}. Decreases of exchangeable cations due to acidification were reported also by (Singh, 1985), Morrison (1984), McColl and Firestone (1987), Cheong (1987), Kim and Lee (1988), Carlson and Ragsdale (1988), Schulze (1989), Weissen *et al.* (1990), Nygaard and Abrahamsen (1991).

It might be expected that in the long term, as cations in soil solution are leached from the soil, more exchangeable cations will move in the soil solution and will be removed thus intensifying the process of loss of exchangeable cations. As base cation export proceeds, the base saturation decreases and finally this not only enhances the sensitivity of the soil to further acidification, but also leads to nutrient impoverishment (Ulrich and Pankrath, 1983; Reuss and Johnson, 1986; Tomlinson *et al.*, 1990). It is also possible that in time part of those key elements would be simply stripped off soil particles (Pokojska, 1987), leading to calcium, magnesium and potassium deficiencies.

The observed changes in soil chemistry suggest that our light soil will probably be more vulnerable to acid rain contamination mainly because of its lower buffer capacity and lower base saturation (Malmer, 1976; Reuss and Johnson, 1986).

5. 2. PLANT CHARACTERISTICS

Growth can be considered the end product of a chain of complex processes both within the tree and its environment. Thus, in general, any change in the environment leads to changes in physiological processes which, in turn, are reflected in growth and development.

For the 11-week treatment period in our study both acid rain and drought and their interaction had a significant influence on jack pine and balsam poplar growth and development.

At this early stage of their development and for this relatively short treatment period acid rain had a positive effect on height and diameter growth. In both soils, plants treated with acid rain were the tallest and had the greatest diameters. Similar results are reported for other species by Lee and Weber (1979), Tveite (1980, after Morrison, 1984), Schier (1987),Temple (1988), Becker and Neighbour(1988), Lee *et al*, (1990a,b). In our case this stimulation can probably be attributed to the fertilizing effect of nitrogen and sulphur. Moreover, it has been shown that the composition and the dosage of the rain applied are also very important. When the acid rain consists of H_2SO_4 alone, height growth is inhibited (Wood and Bormann, 1974), but when it consists also HNO_3 and HCl, it is stimulated (Wood and Bormann, 1977). Increased doses of acid rain also can reduce height growth (Cizkova, 1987).

Although plants treated with acid rain had the greatest diameters, this growth parameter was less strongly affected by acid rain than height growth. It is well known that different growth parameters have different degrees of sensitivity. Often there is an appreciable difference in the degree to which the response is affected (Kozlowski and Constantinidou, 1986). Reduced cambial growth for conifers and broadleaf species is reported when air pollutants or acid rain are applied in such a way that the aboveground parts of the plants are also affected. In such cases SO_2 (Carlson and Bazzaz, 1977; Tsukahara *et al.*, 1984, 1985, after Kozlowski and Constantinidou, 1986), mixtures of SO_2 and NO_x (Phillips *et al.*, 1977 *a, b*; Navratil and McLaughlin, 1979), and mixtures of O_3 and Al (Schier *et al.*,

1990) led to considerable reductions in cambial growth. In all cases however, the plants were exposed to pollutants for relatively long periods of time.

Stimulation of diameter growth is usually observed in short-term experiments in which acid rain has a beneficial effect on growth in general (Temple, 1988). This is because cambial growth and its periodicity are determined by the coordinated interplay of environmental factors, the internal physiological processes and the food reserves of the plant. Also, cambial growth is strongly correlated with leaf renewal processes in the tree and is believed to be controlled by growth hormones (Kozlowski, 1962). As K and Mg are very important in these relationships, the decrease of these ions in the soil may be responsible to some extent for the smaller stimulation of diameter compared to height growth (Tomlinson *et al.*, 1990).

Acid rain not only stimulated height and diameter growth, but also root growth and the production of biomass. In both soils, plants watered with acid rain had larger root systems and produced more biomass than plants in the other treatments. Acid rain had no effect only on the production of belowground biomass of pine in the heavy soil. However, generally poplar cuttings developed less in number, less branched, but thicker roots. Pine seedlings had more in number, more branched, but much thinner roots. This is understandable, as it is well known that root growth varies greatly with species and environmental conditions and depends on the origin of the roots, the stage of development and the branching order (Kozlowski, 1971). On the other hand, in such an early phase of plant development, fine roots are very important. In contrast to growth of main roots, growth and turnover of fine roots seem largely independant of shoot growth. Such fine root growth is more a function of root environment

(Mooney *et al.*, 1990). So, when the nutrient balance of the soil solution is altered, this leads to changes in root growth and development which are reflected in the overall performance of the species. Our findings do not correspond to the majority of the reports in the literature related to the production of biomass. Many studies, mostly with seedlings, document inhibitory effects of environmental pollutants on dry weight increment of both aboveground and belowground parts of woody plants (Suwannapinunt and Kozlowski, 1980; Marshall and Furnier, 1981; Chappelka and Chevone, 1986). Reduction of dry weight increment of roots but not of shoots and leaves has also been reported (Suwannapinunt and Kozlowski, 1980; Shanklin and Kozlowski, 1984; Nosko *et al.*, 1988). This may be due to a difference in the experimental design. In all of the studies cited the pollutants, dry or wet, were applied to both aboveground parts and soils, which means that there was a direct effect of the pollutants on the leaves and shoots. In our case acid rain was applied through irrigation water to the soil only, so its influence on the aboveground parts was only indirect, through the changes in soil chemistry. The increased supply of nitrogen may have stimulated the production of biomass. This was noticed in a similar experiment by Temple (1988). However, acidic deposition not only enriches the soil with nitrogen, but also increases the amount of exchangeable Al^{+++} and decreases base saturation, leading to an unbalanced nutrient supply (Beusichem, 1990). First, Al^{+++} itself is toxic. When it reaches its site of action within the cell it causes disordered metabolism (Tomlinson *et al.*, 1990). Second, it is plausible that Al^{+++} blocks the uptake of Ca^{++} and Mg^{++}, but not of K^{+}, thus enhancing the negative consequences of leaching. This is possible because there are separate pathways for the entry to the roots of the divalent and monovalent nutrient cations. Moreover, calcium deficiency is known to cause increased branching of the roots (Tomlinson *et al.*, 1990). These changes and the species variation in response to the altered soil conditions can explain the increased production of biomass and development of root surface area in plants treated with acid rain as well as the differences between the two species.

As a result of the changes due to the application of acid rain, the shoot : root ratio was generally shifted in favour of the shoots. In our opinion such a stimulation is more likely to be temporary, possibly followed later by an adverse influence, because:

(1) unfavourable changes in soil chemistry have already started and will probably continue and become even more serious with time;

(2) the excessive content of mineral nitrogen, and to some extent of sulfate, in the soil also may inhibit the formation of new lateral roots and mycorrhizae and alter the shoot : root ratio in favour of the shoots (Ekwebelam and Reid, 1984; Esher *et al.*,1992);

(3) acid rain causes an initial increase in the rate of cation nutrient uptake as a result of the increase of cation concentration in soil solution (Johnson and Ball, 1990/91); and

(4) the plants in this early stage of their development had not reached a critical level of "over-saturation" and nitrogen was still acting as a fertilizer.

In both soils, drought had a strong adverse effect on plant growth and development. Plants subjected to drought were shorter, with smaller stem diameters, produced less aboveground and belowground biomass and developed smaller root surface areas. Those unfavourable changes were more strongly expressed in the light soil. Apparently this was due to its texture. It contained more sand, had limited water-holding capacity, and dehydrated easier and faster (Kramer, 1983). Exposure to water stress involves mechanical stress as well as serious dehydration (Fitter and Hay, 1987). As a result, cell and leaf expansion are suppressed (Squire *et al.*, 1987; Fitter and Hay, 1987). Changes in the concentration of major nutrients in the phloem affect both the nutrition of leaves and the hormonal conditions in the xylem and the shoot (Mooney *et al.*, 1990). Together these cause adverse changes in a number of physiological processes and consequently lead to reduction in growth. However, the negative changes in plant growth and development are probably due not only to the direct effect of drought, but also to the indirect effect of the altered soil solution chemistry, as a result of which water and nutrient uptake can decrease (Schulze, 1989). The decrease in uptake is probably due to decrease of root extention rather than to decreased initiation of new roots (Squire *et al.*, 1987). It has been reported that shoot growth is more sensitive to water stress and is more strongly inhibited than root growth due to transpiration (Kramer, 1983; Langerud and Sandvik, 1988). However, our results support the reports for more strongly affected root growth (Seiler and Johnson, 1988; Becker and Neighbour, 1988), which is reflected in an increase in the shoot : root ratio and disturbance of the ability to balance root and shoot growth.

As water is essential for plant growth, development and survival, it was interesting to see how the stress factors affected the water balance of the experimental plants. Water movement through the soil-plant-atmosphere continuum occurs along a path of decreasing potential energy. The resistance is greater in the soil than in the tree and is maximal in the transition from the leaves to the atmosphere where water changes from liquid to vapour. Transpirational water loss from the leaves of a plant growing in wet soil progressively reduces the soil water content and the water potential of the soil. Associated with these changes is a reduction in the water potential and water content of the plant resulting in an increased internal water deficit. Hence, on a day-to-day basis, there is an overall decline in the water potential of a plant growing in drying soil (Kozlowski, 1979). In our study all plants behaved according to this model and developed higher water deficits in drying soil.

All plants previously watered with acid rain developed lower water deficits than controls. This was most probably due to the fact that plants watered with acid rain developed root systems with larger root surface areas and better ability to supply water. Furthermore, a plant absorbs, at least in small amounts, every element presented to it. When more of a particular element is provided, its concentration in the plant usually increases and the levels of some other elements fall (Sutcliffe and Baker, 1976). It is plausible then that an increased supply of nitrogen will lead to increased levels of this element in plant tissues and consequently to changes in nitrogen metabolism. So, it is possible that main products of nitrogen metabolism such as proline and ABA, which are very important in water deficit sensing and probably in drought resistance, might have been affected too. This suggestion has to be examined in future experiments.

The changes in the transpiration rate and diffusive resistance in our experiment were predictable. Transpiration rate of well watered plants is controlled by internal factors such as leaf area, leaf structure and stomatal behavior and by a number of environmental factors, including temperature, solar radiation, humidity, wind (Kramer, 1983). It was not a surprise then that in all watered cuttings transpiration rate was almost the same during the whole measurement period, while in cuttings subjected to drought it decreased. Generally, the transpiration rate at a given vapour pressure deficit is determined by the sum of stomatal and boundary layer resistances. In turn stomatal resistance is determined by the interplay of a complex array of factors such as irradiance, CO_2 level, water stress, humidity, wind, growth substances (Fitter and Hay, 1987). The opening and closing of stomata is mainly controlled by the influx and efflux of K^+ to and from the guard cells, higher concentration inducing water uptake by guard cells from adjacent cells and thus stomatal opening (Tomlinson *et al.*, 1990). The altered concentration of exchangeable K^+ due to acid rain might be one reason for the higher transpiration rates in cuttings watered with acid rain. Another reason is the better water absorption. Due to the higher input of nitrogen cuttings watered with acid rain developed bigger root systems. Moreover, in those cuttings the shoot : root ratios were more favourable. All these are important because absorption commonly lags behind transpiration (Kramer, 1983).

Cuttings subjected to drought had a reduced transpiration rate and growth which can be attributed to low soil moisture and to reduced root growth (Squire *et al.*, 1987; Seiler and Johnson, 1988; Griueu *et al.*, 1988). However, the latest was probably due much more to decrease in root extention than to a reduction in the initiation of new roots, an effect enhanced by increase of soil nitrogen (Squire *et al.*, 1987). The effect of acid rain on the rate of transpiration and diffusive resistance in our poplar cuttings suggests that acid rain does not seem to enhance the species sensitivity to drought, an effect often attributed to this stress factor (Kozlowski and Constantinidou, 1986; Becker and Neighbour, 1988; Barnes *et al.*, 1990). This is probably due to our experimental design. Acid rain was applied only to the soil and there was no direct effect whatsoever on the leaves.

The lower transpiration rate at the end of the treatment period can be partly attributed to the conditioning effect of drought (Squire *et al.*, 1987; Seiler and Johnson, 1988). It has been reported that water stress modifies the stomatal behavior and produces a degree of stomatal sensitivity to decreasing leaf water potential (Penfold, 1992). On the other hand, there was probably some stabilizing of the process with age and maybe some changes in the environmental conditions at the time the measurements were made.

The results from the measurements of fluorescense parameters suggest that acid rain may have a slightly stimulated photosynthesis. This was due, on one hand, to the increased input of nitrogen, and, on the other hand, to the beneficial effect of acid rain to other physiological processes. As pointed out earlier, plants treated with acid rain had more aboveground biomass, bigger root systems, lower water saturation deficits and higher rates of transpiration. All these are important factors in maintaining photosynthesis at a higher level. Besides, it has been reported that acid rain does not cause a decrease in chlorophyll content in jack pine (Abouguendia and Bascak, 1987). The differences between the two tree species are probably due to variation in tolerance of their photochemical apparatus. Similar conclusions were also made by Havaux *et al.* (1988). According to Ogren (1990), leaves of different growth history can show different photosynthetic capacities as well, which result from different amounts of chloroplasts per leaf surface area.

The other stress factor in our experiment, drought, reduced photosynthesis. This was no surprise because it is well known that even moderately low water potential affects photosynthesis in two ways, *vic.* (1) inhibition of O2 evolution by chloroplasts; and (2) closure of stomata (Boyer and Bowen, 1970). Lower turgor, increased concentration of solutes and chemical compounds coming from the roots together with the direct effect of soil drying have all been shown to reduce photosynthesis (Blackman and Davies, 1985; Kaiser, 1987; Zang and Davies, 1989; Chaves, 1991). On the other hand, stomatal closure, as a response to the limited water reserves in the leaves, not only protects the plant against water loss, but also simultaneously restricts carbon assimilation (Chaves, 1991). The higher water deficit in all seedlings and cuttings subjected to drought and their reduced rates of transpiration are reasons for the slower rate of photosynthesis.

Generally, when acid rain and drought were applied together, acid rain reduced the adverse effect of drought on photosynthesis. This was again probably due to the increased supply of nitrogen, which maintained the same or increased the level of nitrogen in the tissues. This is important because even a slight decrease in nitrogen status enhances the effects of drought (Ogren, 1988, 1990).

Despite the effects of acid rain and drought, soil type was the most significant factor affecting plant growth and development. Both pine seedlings and poplar cuttings performed better in the light soil, which offered more favourable growth conditions. Besides, jack pine is typically a tree of light sandy soils and balsam poplar develops best on moist, often rich and deep sandy and gravelly soils. However, the light soil seems to be more vulnerable to acid rain contamination. The changes in soil chemistry, detected in our study, may be considered as an indication of serious future impact of acid rain on soils. In the long term in nature these changes can possibly lead to changes in soil biota and biological processes and alteration of mycorrhiza. All these changes are also indication of "site sensitivity", which is significant from the viewpoint of soil management. Obviously, in future forest regeneration and management attention should be paid to site sensitivity to acid precipitation and research must continue to clarify this serious problem.

In our opinion the stimulating effect of acid rain in this short term experiment can not be considered as a beneficial effect of acid rain on early forest growth. We have some concerns:

1. The higher input of nitrogen and sulphur via acid rain may be accompanied by adverse changes in soil chemistry. Increased aluminum may cause leaching of important nutrients from the soil, such as calcium, magnesium, potassium which could finally lead to nutrient deficiencies. At the same time, increased amounts of soluble aluminum, manganese and other metals may reach toxic concentrations, causing damage to root systems, thus affecting the plant's ability to take up nutrients and water, and hence - plant growth and development.

2. In nature acidic deposition directly affects both the aboveground and the belowground parts of plants.

3. Trees are long living organisms and an excess of nitrogen in the soil does not mean unquestionably positive effects on tree growth. After the demands for nitrogen are satisfied, the ecosystem becomes over-saturated with nitrogen which can have a distinct adverse effect on tree growth and development. According to Ulrich's hypothesis and the findings of Abrahamsen, there are three sequential phases, resulting from acidic

deposition. The first phase is dominated by the growth-stimulating effect of nitrogen compounds now present in the atmosphere and rain. Phase two is characterized by the depletion of nutrient "base cations" giving rise to deficiency of some elements such as magnesium. Phase three is characterized as the ultimate stage, where toxic levels of aluminum and/or of heavy metals can result in premature tree and forest death (Tomlinson *et al.*, 1990). Moreover, according to the ammonium hypothesis of Nihlgard (1985) excess of nitrogen can be harmful to tree and forest health. Nitrogen taken up is transformed into ammonium, amines or amides and soluble carbohydrates are consumed. Thus, toxic nitrogen concentrations might be reached in the leaves or needles and shoot damage might appear. Also, due to decreased amounts of soluble carbohydrates root growth is decreased. In general the tolerance of plants to an ample supply of ammonium is low, whereas the tolerance to nitrates is high, but in excess both can be toxic to plants. Ammonium can cause acidification of the plant's rhizosphere, potassium and calcium deficiencies, decreased plant water uptake and leaf water potential, and metabolic disturbances which lead to yield reductions (Haynes, 1986). Although a plant normally adapts to a high level of nitrate supply by storing it in vacuoles of plant tissue for future reduction and use, an excess of nitrates can be toxic. However, the mechanism of this toxicity is still unknown (Haynes, 1986). All these and the related effects become more strongly expressed when nitrogen in the soil or in leaves becomes "over-saturated" in relation to water and several mineral nutrients like magnesium, potassium and phosphorus, which are needed for ammonium assimilation or protein synthesis (Nihlgard, 1985). So, forests growing on high-fertility soils may stand heavier loading of nitrogen than forests growing on low-fertility dry soils.

4. The faster earlier growth due to an increased supply of nitrogen might actually be very dangerous and later may have negative consequences. On one hand, the faster the growth, the greater the risk of damages from air pollution (Kozlowski and Constantinidou, 1986). And in nature acid rain is normally accompanied by other pollutants like ozone, for example. On the other hand, the inner hormone balance is disturbed. Plants that have grown faster and have formed large cells with high volume are later easily attacked by wind, drought and parasites. Moreover, due to decreased amounts of soluble carbohydrates the frost hardiness, mainly of conifers, may be seriously imperiled (Morrison, 1984; Nihlgard, 1985).

In our experiment both species responded to the soil conditions and the stress factors in a similar way. Although differences between northern and southern provenances of jack pine have been shown to exist (Yeatman, 1974), in our study provenance was much more important for balsam poplar. Cuttings from the southern provenance grew faster and better, they had lower water deficit and higher rates of transpiration and photosynthesis. This was no surprise as representatives from the southern provenance are known to have longer and wider leaves and greater biomass than representatives from the northern provenances. Generally, plants with larger individual leaf areas and weights also are taller, with more leaves per stem and larger root, shoot and leaf weights (Penfold, 1992).

The results of our experiment show that acid rain with pH as low as 3.0 was not directly harmful to early growth and development of jack pine and balsam poplar. It even reduced the adverse effects of drought. However, this was a short term greenhouse experiment. The detected changes in soil chemistry and the accelerated early growth might be considered also as an indication for potential unfavourable effects of acid rain in the long term, no matter the beneficial effect in the short term. Therefore, as trees are long living organisms, their response to these stress factors, and particularly to acid rain, in the long term is also very important.

For more decisive conclusions future research is needed to confirm these findings in the field. Obviously, despite of all difficulties, long-term experiments are necessary to clarify the impact of acid rain on forest tree growth and development.

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APPENDIX I

Table I. Analysis of variance for the soil texture.

Fractions		Sand					Clay					Silt			
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
								poplar							
Main effects	1976.817	4	494.204	131.330	.000	3347.443	4	836.861	1958.299	.000	176.538	4	44.134	19.799	.000
AR	.138	1	.138	.037	.851	2.371	1	2.371	5.548	.032	1.005	1	1.005	.451	.512
D	2.398	1	2.398	.637	.436	3.843	1	3.843	8.994	.008	.310	1	.310	.139	.714
ST	1974.119	1	1974.119	524.604	.000	3339.284	1	3339.284	7814.103	.000	174.518	1	174.518	78.289	.000
PR	.162	1	.162	.043	.838	1.945	1	1.945	4.552	.049	.705	1	.705	.316	.582
2-way interactions	1.839	6	.306	.081	.997	7.576	6	1.263	2.955	.039	11.119	6	1.853	.831	.563
AR D	.520	1	.520	.138	.715	.044	1	.044	.104	.752	.575	1	.575	.258	.618
AR ST	.293	1	.293	.078	.784	.554	1	.554	1.296	.272	1.236	1	1.236	.555	.467
AR PR	.084	1	.084	.022	.883	1.276	1	1.276	2.986	.103	2.514	1	2.514	1.128	.304
D ST	.252	1	.252	.067	.799	2.874	1	2.874	6.725	.020	1.810	1	1.810	.812	.381
D PR	.466	1	.466	.124	.730	2.767	1	2.767	6.475	.022	4.844	1	4.844	2.173	.160
ST PR	.224	1	.224	.060	.810	.060	1	.060	.141	.712	.139	1	.139	.062	.806
3-way interactions	3.402	4	.850	.226	.920	4.191	4	1.048	2.452	.088	1.296	4	.324	.145	.962
AR D ST	.296	1	.296	.079	.783	.226	1	.226	.529	.477	.055	1	.055	.025	.877
AR D PR	.332	1	.332	.088	.770	.000	1	.000	.001	.981	.538	1	.538	.241	.630
AR ST PR	.320	1	.320	.085	.774	1.484	1	1.484	3.471	.081	.682	1	.682	.306	.58
D ST PR	2.453	1	2.453	.652	.431	2.481	1	2.481	5.805	.028	.021	1	.021	.009	.925
4-way interactions	.738	1	.738	.196	.664	1.284	1	1.284	3.005	.102	.194	1	.194	.087	.772
AR D ST PR	.738	1	.738	.196	.664	1.284	1	1.284	3.005	.102	.194	1	.194	.087	.772

Table I, cont.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Explained	1982.796	15	132.186	35.127	.000	3360.493	15	224.033	524.249	.000	189.146	15	12.610	5.657	.001
Residual	60.209	16	3.763			6.837	16	.427			35.666	16	2.229		
Total	2043.005	31	65.903			3367.331	31	108.624			224.812	31	7.250		
										pine					
AR	.256	1	.256	.164	.691	.664	1	.664	.681	.421	.226	1	.226	.143	.71
D	1.403	1	1.403	.901	.357	1.324	1	1.324	1.359	.261	.012	1	.012	.008	.93
ST	2016.125	1	2016.125	1295.528	.000	136.331	1	136.331	139.879	.000	3217.424	1	3217.424	2039.923	.00
PR	.898	1	.898	.577	.459	1.012	1	1.012	1.038	.323	4.433	1	4.433	2.810	.11
2-way interactions	1.652	6	.275	.177	.979	6.081	6	1.014	1.040	.436	6.018	6	1.003	.636	.70
AR D	.026	1	.026	.017	.898	.081	1	.081	.083	.777	.385	1	.385	.244	.62
AR ST	.813	1	.813	.522	.480	1.244	1	1.244	1.277	.275	.150	1	.150	.095	.76
AR PR	.033	1	.033	.021	.887	.888	1	.888	.911	.354	.355	1	.355	.225	.64
D ST	.000	1	.000	.000	.989	2.327	1	2.327	2.388	.142	1.936	1	1.936	1.227	.28
D PR	.679	1	.679	.436	.518	.100	1	.100	.103	.753	.426	1	.426	.270	.61
ST PR	.101	1	.101	.065	.802	1.441	1	1.441	1.478	.242	2.767	1	2.767	1.754	.20
3-way interactions	5.359	4	1.340	.861	.508	6.391	4	1.598	1.639	.213	1.625	4	.406	.258	.90
AR D ST	3.328	1	3.328	2.139	.163	4.797	1	4.797	4.922	.041	.283	1	.283	.180	.67
AR D PR	.925	1	.925	.594	.452	.998	1	.998	1.024	.327	.019	1	.019	.012	.91
AR ST PR	.242	1	.242	.155	.699	.518	1	.518	.531	.477	1.077	1	1.077	.683	.42
D ST PR	.865	1	.865	.556	.467	.079	1	.079	.081	.780	.247	1	.247	.156	.69
4-way interactions	.442	1	.442	.284	.601	3.400	1	3.400	3.488	.080	1.026	1	1.026	.651	.43
AR D ST PR	.442	1	.442	.284	.601	3.400	1	3.400	3.488	.080	1.026	1	1.026	.651	.43
Explained	2026.134	15	135.076	86.797	.000	155.204	15	10.347	10.616	.000	3230.764	15	215.384	136.559	.00
Residual	24.899	16	1.556			15.594	16	.975			25.236	16	1.577		
Total	2051.034	31	66.162			170.798	31	5.510			3256.000	31	105.032		

Table II. Analysis of variance for the total soil organic matter.

Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	F pr
			poplar					pine		
Main effects	20.500	4	5.125	2.562	.079	30.500	4	7.625	4.357	.014
AR	18.000	1	18.000	9.000	.008	28.125	1	28.125	16.071	.001
D	2.000	1	2.000	1.000	.332	1.125	1	1.125	.643	.434
ST	.500	1	.500	.250	.624	.125	1	.125	.071	.793
PR	.000	1	.000	.000	1.000	1.125	1	1.125	.643	.434
2-way interactions	5.500	6	.917	.458	.829	1.750	6	.292	.167	.982
AR D	2.000	1	2.000	1.000	.332	.125	1	.125	.071	.793
AR ST	.500	1	.500	.250	.624	.125	1	.125	.071	.793
AR PR	2.000	1	2.000	1.000	.332	1.125	1	1.125	.643	.434
D ST	.500	1	.500	.250	.624	.125	1	.125	.071	.793
D PR	.000	1	.000	.000	1.000	.125	1	.125	.071	.793
ST PR	.500	1	.500	.250	.624	.125	1	.125	.071	.793
3-way interactions	1.500	4	.375	.187	.941	2.500	4	.625	.357	.835
AR D ST	.500	1	.500	.250	.624	.125	1	.125	.071	.793
AR D PR	.000	1	.000	.000	1.000	.125	1	.125	.071	.793
AR ST PR	.500	1	.500	.250	.624	1.125	1	1.125	.643	.434
D ST PR	.500	1	.500	.250	.624	1.125	1	1.125	.643	.434
4-way interactions	.500	1	.500	.250	.624	.125	1	.125	.071	.793
AR D ST PR	.500	1	.500	.250	.624	.125	1	.125	.071	.793
Explained	28.000	15	1.867	.933	.551	34.875	15	2.325	1.329	.289
Residual	32.000	16	2.000			28.000	16	1.750		
Total	60.000	31	1.935			62.875	31	2.028		

Table III. Analysis of variance for the composition of the soil organic matter.

Elements	Carbon					Hydrogen					Nitrogen				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
									poplar						
Main effects	.954	4	.238	14.956	.000	.002	4	.000	.396	.808	.004	4	.001	10.179	.000
AR	.000	1	.000	.010	.923	.000	1	.000	.110	.745	.000	1	.000	2.286	.150
D	.012	1	.012	.778	.391	.000	1	.000	.049	.828	.000	1	.000	1.286	.274
ST	.868	1	.868	54.446	.000	.000	1	.000	.439	.517	.003	1	.003	36.571	.000
PR	.073	1	.073	4.589	.048	.001	1	.001	.988	.335	.000	1	.000	.571	.461
2-way interactions	.144	6	.024	1.501	.240	.013	6	.002	2.073	.114	.001	6	.000	1.214	.349
AR D	.008	1	.008	.510	.485	.002	1	.002	2.061	.170	.000	1	.000	1.286	.274
AR ST	.037	1	.037	2.329	.146	.000	1	.000	.305	.588	.000	1	.000	.517	.461
AR PR	.003	1	.003	.188	.670	.000	1	.000	.439	.517	.000	1	.000	.571	.461
D ST	.031	1	.031	1.921	.185	.006	1	.006	5.902	.027	.000	1	.000	1.286	.274
D PR	.060	1	.060	3.788	.069	.001	1	.001	.988	.335	.000	1	.000	1.286	.274
ST PR	.004	1	.004	.268	.612	.003	1	.003	2.744	.177	.000	1	.000	2.286	.150
3-way interactions	.181	4	.045	2.835	.059	.003	4	.001	.677	.618	.000	4	.000	1.107	.387
AR D ST	.024	1	.024	1.484	.241	.000	1	.000	.012	.913	.000	1	.000	3.571	.077
AR D PR	.006	1	.006	.397	.538	.000	1	.000	.000	1.000	.000	1	.000	.143	.710
AR ST PR	.027	1	.027	1.696	.211	.001	1	.001	1.220	.286	.000	1	.000	.571	.461
D ST PR	.124	1	.124	7.763	.013	.002	1	.002	1.476	.242	.000	1	.000	.143	.710
4-way interactions	.009	1	.009	.593	.452	.000	1	.000	.049	.828	.000	1	.000	.143	.710
AR D ST PR	.009	1	.009	.593	.452	.000	1	.000	.049	.828	.000	1	.000	.143	.710
Explained	1.287	15	.086	5.384	.001	.017	15	.001	1.119	.412	.005	15	.000	3.505	.009
Residual	.255	16	.016			.016	16	.001			.001	16	.000		
Total	1.542	31	.050			.033	31	.001			.006	31	.000		

Table III, cont.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
									<u>pine</u>						
Main effects	.168	4	.042	1.801	.178	.031	4	.008	2.957	.053	.007	4	.002	4.481	.013
AR	.014	1	.014	.601	.449	.001	1	.001	.266	.613	.000	1	.000	.618	.443
D	.012	1	.012	.498	.490	.001	1	.001	.200	.661	.000	1	.000	.069	.797
ST	.033	1	.033	1.421	.251	.023	1	.023	8.530	.010	.007	1	.007	16.863	.001
PR	.109	1	.109	4.684	.046	.008	1	.008	2.835	.112	.000	1	.000	.374	.549
2-way interactions	.197	6	.033	1.406	.272	.011	6	.002	.721	.639	.001	6	.000	.445	.838
AR D	.006	1	.006	.271	.610	.001	1	.001	.266	.613	.000	1	.000	.069	.797
AR ST	.006	1	.006	.248	.625	.000	1	.000	.058	.813	.000	1	.000	.191	.668
AR PR	.019	1	.019	.794	.386	.003	1	.003	1.135	.303	.000	1	.000	.374	.549
D ST	.121	1	.121	5.199	.037	.007	1	.007	2.608	.126	.000	1	.000	.191	.668
D PR	.006	1	.006	.271	.610	.001	1	.001	.200	.661	.000	1	.000	.924	.351
ST PR	.039	1	.039	1.651	.217	.000	1	.000	.058	.813	.000	1	.000	.924	.351
3-way interactions	.074	4	.019	.795	.546	.003	4	.001	.266	.896	.001	4	.000	.511	.728
AR D ST	.000	1	.000	.016	.900	.000	1	.000	.001	.973	.000	1	.000	.008	.931
AR D PR	.008	1	.008	.322	.578	.001	1	.001	.341	.567	.001	1	.001	1.290	.273
AR ST PR	.046	1	.046	1.961	.180	.001	1	.001	.521	.481	.000	1	.000	.374	.549
D ST PR	.021	1	.021	.879	.362	.001	1	.001	.200	.661	.000	1	.000	.374	.549
4-way interactions	.001	1	.001	.023	.882	.002	1	.002	.861	.367	.000	1	.000	.191	.668
AR D ST PR	.001	1	.001	.023	.882	.002	1	.002	.861	.367	.000	1	.000	.191	.668
Explained	.439	15	.029	1.256	.327	.048	15	.003	1.205	.357	.009	15	.001	1.522	.207
Residual	.373	16	.023			.042	16	.003			.007	16	.000		
Total	.813	31	.026			.090	31	.003			.016	31	.001		

Table IV. Analysis of variance for the soil pH measured in water and in 0.01M $CaCl_2$.

	pH in water					pH in 0.01M CaC12				
Source of variatrion	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10.	11
					poplar					
Main effects	14.041	4	3.510	337.827	.000	30.959	4	7.740	2107.851	.000
AR	.619	1	.619	59.556	.000	.236	1	.236	64.362	.000
D	.001	1	.001	.068	.798	.000	1	.000	.021	.886
ST	13.326	1	13.326	1282.474	.000	30.713	1	30.713	8364.447	.000
PR	.096	1	.096	9.211	.008	.009	1	.009	2.574	.128
2-way interactions	.343	6	.057	5.501	.003	.041	6	.007	1.865	.149
AR D	.001	1	.001	.068	.798	.002	1	.002	.532	.476
AR ST	.144	1	.144	13.902	.002	.034	1	.034	9.383	.007
AR PR	.066	1	.066	6.323	.023	.002	1	.002	.532	.476
D ST	.034	1	.034	3.316	.087	.000	1	.000	.021	.886
D PR	.096	1	.096	9.211	.008	.001	1	.001	.191	.668
ST PR	.002	1	.002	.188	.670	.002	1	.002	.532	.476
3-way interactions	.142	4	.036	3.421	.033	.019	4	.005	1.298	.313
AR D ST	.041	1	.041	3.977	.063	.018	1	.018	4.787	.044
AR D PR	.049	1	.049	4.699	.046	.000	1	.000	.191	.668
AR ST PR	.018	1	.018	1.692	.212	.000	1	.000	.021	.886
D ST PR	.034	1	.034	3.316	.087	.001	1	.001	.191	.668
4-way interactions	.057	1	.057	5.481	.032	.006	1	.006	1.723	.208

Table IV, cont.

1	2	3	4	5	6	7	8	9	10	11
AR D ST PR	.057	1	.057	5.481	.032	.006	1	.006	1.723	.208
Explained	14.583	15	.972	93.565	.000	31.026	15	2.068	563.301	.000
Residual	.166	16	.010			.059	16	.004		
Total	14.749	31	.476			31.084	31	1.003		
					<u>pine</u>					
Main effects	16.765	4	4.191	133.450	.000	30.322	4	7.580	1228.215	.000
AR	.661	1	.661	21.055	.000	.144	1	.144	23.405	.000
D	.000	1	.000	.010	.922	.049	1	.049	7.911	.013
ST	16.103	1	16.103	512.726	.000	30.128	1	30.128	4881.532	.000
PR	.000	1	.000	.010	.922	.000	1	.000	.013	.912
2-way interactions	.385	6	.064	2.041	.119	.067	6	.011	1.819	.159
AR D	.090	1	.090	2.876	.109	.041	1	.041	6.696	.020
AR ST	.228	1	.228	7.254	.016	.009	1	.009	1.532	.234
AR PR	.015	1	.015	.488	.495	.002	1	.002	.316	.582
D ST	.020	1	.020	.637	.437	.013	1	.013	2.139	.163
D PR	.020	1	.020	.637	.437	.001	1	.001	.114	.740
ST PR	.011	1	.011	.358	.558	.001	1	.001	.114	.740
3-way interactions	.009	4	.002	.072	.990	.042	4	.010	1.684	.203
AR D ST	.005	1	.005	.159	.695	.004	1	.004	.620	.442
AR D PR	.001	1	.001	.040	.884	.013	1	.013	2.139	.163
AR ST PR	.000	1	.000	.000	1.000	.002	1	.002	.316	.582
D ST PR	.003	1	.003	.090	.769	.023	1	.023	3.658	.074
4-way interactions	.008	1	.008	.249	.625	.009	1	.009	1.532	.234
AR D ST PR	.008	1	.008	.249	.625	.009	1	.009	1.532	.234
Explained	17.166	15	1.144	36.439	.000	30.440	15	2.029	328.803	.000
Residual	.503	16	.031			.099	16	.006		
Total	17.669	31	.570			30.539	31	.985		

Table V. Analysis of variance for the cation exchange capacity of the heavy and light soils used in the experiment.

Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
			poplar					pine		
Main effects	133.000	4	33.250	15.647	.000	111.000	4	27.750	14.800	.000
AR	72.000	1	72.000	33.872	.000	60.500	4	60.500	32.267	.000
D	.000	1	.000	.000	1.000	.000	1	.000	.000	1.000
ST	60.500	1	60.500	28.471	.000	50.000	1	50.000	26.667	.000
PR	.500	1	.500	.235	.634	.500	1	.500	.267	.613
2-way interactions	8.000	6	1.333	.627	.706	3.000	6	.500	.267	.945
AR D	2.000	1	2.000	.941	.346	2.000	1	2.000	1.067	.317
AR ST	.500	1	.500	.235	.634	.000	1	.000	.000	1.000
AR PR	.500	1	.500	.235	.634	.500	1	.500	.267	.613
D ST	.500	1	.500	.235	.634	.500	1	.500	.267	.613
D PR	4.500	1	4.500	2.118	.165	.000	1	.000	.000	1.000
ST PR	.000	1	.000	.000	1.000	.000	1	.000	.000	1.000
3-way interactions	3.000	4	.750	.353	.838	1.000	4	.250	.133	.968
AR D ST	.500	1	.500	.235	.634	.500	1	.500	.267	.613
AR D PR	.500	1	.500	.235	.634	.000	1	.000	.000	1.000
AR ST PR	.000	1	.000	.000	1.000	.000	1	.000	.000	1.000
D ST PR	2.000	1	2.000	.941	.346	.500	1	.500	.267	.613
4-way interactions	.000	1	.000	.000	1.000	.500	1	.500	.267	.613
AR D ST PR	.000	1	.000	.000	1.000	.500	1	.500	.267	.613
Explained	144.000	15	9.600	4.518	.002	115.500	15	7.700	4.107	.004
Residual	34.000	16	2.125			30.000	16	1.875		
Total	178.000	31	5.742			145.500	31	4.610		

Table VI. Analysis of variance for the base saturation of the heavy and light soils used in the experiment.

Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
	poplar					pine				
Main effects	4277.125	4	1069.281	13.915	.000	3873.625	4	968.406	16.475	.000
AR	3762.781	1	3762.781	48.967	.000	3341.531	1	3341.531	56.847	.000
D	22.781	1	22.781	.296	.594	157.531	1	157.531	1.680	.221
ST	457.531	1	457.531	5.954	.027	344.531	1	344.531	5.861	.028
PR	34.031	1	34.031	.443	.515	30.031	1	30.031	.511	.485
2-way interactions	221.938	6	36.990	.481	.813	344.438	6	57.406	.977	.472
AR D	75.031	1	75.031	.976	.338	108.781	1	108.781	1.851	.193
AR ST	19.531	1	19.531	.254	.621	132.031	1	132.031	2.246	.153
AR PR	.031	1	.031	.000	.984	26.281	1	26.281	.447	.513
D ST	47.531	1	47.531	.619	.443	.281	1	.281	.005	.946
D PR	16.531	1	16.531	.215	.649	63.281	1	63.281	1.077	.315
ST PR	63.281	1	63.281	.824	.378	13.781	1	13.781	.234	.635
3-way interactions	188.625	4	47.156	.614	.659	150.625	4	37.656	.641	.641
AR D ST	52.531	1	52.531	.684	.421	47.531	1	47.531	.809	.382
AR D PR	1.531	1	1.531	.020	.890	57.781	1	57.781	.983	.336
AR ST PR	2.531	1	2.531	.033	.858	7.031	1	7.031	.120	.734
D ST PR	132.031	1	132.031	1.718	.208	38.281	1	38.281	.651	.431
4-way interactions	3.781	1	3.781	.049	.827	42.781	1	42.781	.728	.406
AR D ST PR	3.781	1	3.781	.049	.827	42.781	1	42.781	.728	.406
Explained	4691.469	15	312.765	4.070	.004	4411.469	15	294.098	5.003	.001
Residual	1229.500	16	76.844			940.500	16	58.781		
Total	5920.969	31	190.999			5351.969	31	172.644		

Table VII. Analysis of variance for the amount of exchangeable ions in the heavy and light soils used in the experiment

Elements	Al					Ca					K					Mg				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
										poplar										
Main effets	21.508	4	5.377	52.981	.000	670293.111	4	167573.278	515.21	.000	298.359	4	74.590	68.810	.000	4218.834	4	1054.708	183.418	.000
AR	.000	1	.000	.000	.985	2840.130	1	2840.130	8.732	.009	273.780	1	273.780	252.565	.000	301.965	1	301.708	52.513	.000
D	.095	1	.095	.934	.348	273.839	1	273.839	.842	.372	1.394	1	1.394	1.286	.273	2.940	1	2.940	.511	.485
ST	21.395	1	21.395	210.816	.000	667090.465	1	667090.465	2051.016	.000	14.365	1	14.365	13.252	.002	3913.913	1	3913.913	680.643	.000
PR	.018	1	.018	.173	.683	88.678	1	88.678	.273	.609	8.820	1	8.820	8.137	.012	.015	1	.015	.003	.959
2-way nteractions	.341	6	.057	.560	.755	1963.991	6	327.332	1.006	.455	34.877	6	5.813	5.362	.003	74.577	6	12.429	2.162	.102
AR D	.183	1	.183	1.806	.198	122.344	1	122.344	.376	.548	4.162	1	4.162	3.839	.068	24.325	1	24.325	4.230	.056
AR ST	.002	1	.002	.016	.900	1244.132	1	1244.132	3.825	.068	1.163	1	1.163	1.073	.316	.070	1	.070	.012	.913
AR PR	.004	1	.004	.039	.846	176.391	1	176.391	.542	.472	3.578	1	3.578	3.301	.088	.813	1	.813	.141	.712
D ST	.015	1	.015	.145	.709	396.141	1	396.141	1.218	.286	1.194	1	1.194	1.101	.310	35.490	1	35.490	6.172	.024
D PR	.108	1	.108	1.064	.318	23.239	1	23.239	.071	.793	8.222	1	8.222	7.584	.014	13.650	1	13.650	2.374	.143
ST PR	.030	1	.030	.292	.596	1.744	1	1.744	.005	.943	16.560	1	16.560	15.277	.001	.228	1	.228	.040	.845
3-way nteractions	.338	4	.084	.832	.524	1012.437	4	253.109	.778	.555	4.982	4	1.246	1.149	.369	13.479	4	3.370	.586	.677
AR D ST	.031	1	.031	.307	.587	471.475	1	471.475	1.450	.246	.065	1	.065	.060	.810	7.125	1	7.125	1.239	.282
AR D PR	.156	1	.156	1.541	.232	42.389	1	42.389	.130	.723	.819	1	.819	.756	.398	1.240	1	1.240	.216	.649
AR ST PR	.003	1	.003	.027	.872	224.032	1	224.032	.689	.419	3.354	1	3.354	3.094	.098	2.050	1	2.050	.357	.559
D ST PR	.148	1	.148	1.454	.245	274.541	1	274.541	.844	.372	.744	1	.744	.687	.420	3.063	1	3.063	.533	.476
4-way nteractions	.149	1	.149	1.473	.243	256.341	1	256.341	.788	.388	2.132	1	2.132	1.967	.180	4.728	1	4.728	.822	.378
AR D ST P	.149	1	.149	1.473	.243	256.341	1	256.341	.788	.388	2.132	1	2.132	1.967	.180	4.728	1	4.728	.822	.378

Table VII, cont.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Explained	22.336	15	1.489	14.673	.000	673525.880	15	44901.725	138.053	.000	340.351	15	22.690	20.932	.000	4311.617	15	287.441	49.987	.000
Residual	1.624	16	.101			5203.980	16	325.249			17.344	16	1.084			92.005	16	5.750		
Total	23.960	31	.773			678729.860	31	21894.512			357.695	31	11.539			4403.622	31	142.052		
											<u>pine</u>									
ain effects	110.503	4	27.626	225.180	.000	640775.794	4	160193.948	258.070	.000	448.727	4	112.182	87.913	.000	5270.351	4	1317.588	71.917	.000
AR	5.462	1	5.462	44.524	.000	3425.850	1	3425.850	5.519	.032	424.060	1	424.060	332.322	.000	210.638	1	210.638	11.497	.004
D	4.956	1	4.956	40.395	.000	1.240	1	1.240	.002	.965	5.289	1	5.289	4.145	.059	69.325	1	69.325	3.784	.070
ST	100.065	1	100.065	815.641	.000	637235.828	1	637235.828	1026.576	.000	17.302	1	17.302	13.559	.002	4972.538	1	4972.538	271.413	.000
PR	.020	1	.020	.162	.693	112.875	1	112.875	.182	.675	2.076	1	2.076	1.627	.220	17.850	1	17.850	.974	.338
-way teractions	11.148	6	1.858	15.145	.000	2887.639	6	481.273	.775	.601	31.366	6	5.228	4.097	.011	71.454	6	11.909	.650	.690
AR D	3.288	1	3.288	26.798	.000	789.038	1	789.038	1.271	.276	6.239	1	6.239	4.890	.042	14.988	1	14.988	.818	.379
AR ST	4.609	1	4.609	37.572	.000	1825.590	1	1825.590	2.941	.106	11.556	1	11.556	9.056	.008	.475	1	.475	.026	.874
AR PR	.224	1	.224	1.825	.195	33.825	1	33.825	.054	.818	5.064	1	5.064	3.969	.064	.475	1	.475	.026	.874
D ST	2.931	1	2.931	23.893	.000	11.400	1	11.400	.018	.894	3.969	1	3.969	3.110	.097	38.063	1	38.063	2.078	.169
D PR	.094	1	.094	.769	.394	183.840	1	183.840	.296	.594	3.348	1	3.348	2.623	.125	12.878	1	12.878	.703	.414
ST PR	.002	1	.002	.014	.909	43.945	1	43.945	.071	.794	1.190	1	1.190	.932	.349	4.575	1	4.575	.250	.624
-way eractions	4.049	4	1.012	8.250	.001	576.319	4	144.080	.232	.916	3.223	4	.806	.631	.647	11.346	4	2.837	.155	.958
AR D ST	2.722	1	2.722	22.187	.000	440.303	1	440.303	.709	.412	.513	1	.513	.402	.535	4.728	1	4.728	.258	.618
AR D PR	1.090	1	1.090	8.888	.009	106.945	1	106.945	.172	.684	.473	1	.473	.371	.551	2.365	1	2.365	.129	.724
AR ST PR	.201	1	.201	1.639	.219	.000	1	.000	.000	.999	.027	1	.027	.021	.886	2.588	1	2.588	.141	.712
D ST PR	.035	1	.035	.287	.600	29.070	1	29.070	.047	.831	2.210	1	2.210	1.732	.207	1.665	1	1.665	.091	.767
-way eractions	.600	1	.600	4.893	.042	8.715	1	8.715	.014	.907	3.665	1	3.665	2.872	.109	2.940	1	2.940	.160	.694
AR D ST PR	.600	1	.600	4.893	.042	8.715	1	8.715	.014	.907	3.665	1	3.665	2.872	.109	2.940	1	2.940	.160	.694
xplained	126.300	15	8.420	68.632	.000	644248.467	15	42949.898	69.192	.000	486.981	15	32.465	25.442	.000	5356.092	15	357.073	19.490	.000
esidual	1.963	16	.123			9931.825	16	620.739			20.417	16	1.276			293.135	16	18.321		
otal	128.263	31	4.138			654180.292	31	21102.590			507.398	31	16.368			5649.227	31	182.233		

Table VIII. Analysis of variance for the pine height.

Time	Aug 18					Sept 20					Nov 11				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	125.717	4	31.429	41.184	.000	151.547	4	37.887	48.357	.000	266.111	4	66.528	117.475	.000
AR	.753	1	.753	.986	.324	3.118	1	3.118	3.979	.049	14.805	1	14.805	26.143	.000
D	.005	1	.005	.007	.935	.175	1	.175	.223	.638	6.880	1	6.880	12.149	.001
ST	123.533	1	123.533	161.874	.000	147.758	1	147.758	188.593	.000	243.525	1	243.525	430.019	.000
PR	1.426	1	1.426	1.868	.175	.496	1	.496	.633	.429	.901	1	.901	1.591	.211
2-way interactions	6.401	6	1.067	1.398	.226	6.393	6	1.066	1.360	.241	12.427	6	2.071	3.657	.003
AR D	.046	1	.046	.060	.807	.005	1	.005	.007	.936	1.193	1	1.193	2.106	.151
AR ST	.100	1	.100	.131	.718	.055	1	.055	.070	.792	2.633	1	2.633	4.650	.034
AR PR	2.503	1	2.503	3.279	.074	1.680	1	1.680	2.144	.147	.293	1	.293	.517	.474
D ST	.013	1	.013	.017	.898	.113	1	.113	.145	.705	1.475	1	1.475	2.605	.110
D PR	.175	1	.175	.229	.633	.076	1	.076	.097	.756	.271	1	.271	.478	.491
ST PR	3.565	1	3.565	4.672	.034	4.463	1	4.463	5.697	.019	6.563	1	6.563	11.588	.001
3-way interactions	3.614	4	.903	1.184	.324	3.479	4	.870	1.110	.358	2.386	4	.597	1.053	.385
AR D ST	.825	1	.825	1.081	.302	1.628	1	1.628	2.077	.153	.055	1	.055	.097	.756
AR D PR	.753	1	.753	.986	.324	.586	1	.586	.748	.390	2.071	1	2.071	3.657	.059
AR ST PR	1.283	1	1.283	1.682	.198	.825	1	.825	1.053	.308	.230	1	.230	.406	.526
D ST PR	.753	1	.753	.986	.324	.440	1	.440	.562	.456	.030	1	.030	.053	.818
4-way interactions	.338	1	.338	.443	.507	.388	1	.388	.495	.484	.718	1	.718	1.267	.264
AR D ST PR	.338	1	.338	.443	.507	.388	1	.388	.495	.484	.718	1	.718	1.267	.264
Explained	136.071	15	9.071	11.887	.000	161.807	15	10.787	13.768	.000	281.642	15	18.776	33.155	.000
Residual	61.052	80	.763			62.678	80	.783			45.305	80	.566		
Total	197.122	95	2.075			244.485	95	2.363			326.947	95	3.442		

Table IX. Analysis of variance for the pine root collar diameter.

Source of variation	SS	DF	MS	F	Fpr
Main effects	10.089	4	2.522	74.353	.000
AR	.251	1	.251	7.403	.008
D	.849	1	.849	25.040	.000
ST	8.985	1	8.985	264.888	.000
PR	.003	1	.003	.080	.778
2-way interactions	.305	6	.051	1.500	.189
AR D	.002	1	.002	.057	.812
AR ST	.010	1	.010	.289	.592
AR PR	.047	1	.047	1.393	.241
D ST	.006	1	.006	.164	.687
D PR	.070	1	.070	2.060	.155
ST PR	.171	1	.171	5.037	.028
3-way interactions	.082	4	.021	.608	.658
AR D ST	.009	1	.009	.277	.600
AR D PR	.001	1	.001	.026	.873
AR ST PR	.021	1	.021	.628	.430
D ST PR	.051	1	.051	1.500	.224
4-way interactions	.002	1	.002	.068	.795
AR D ST PR	.002	1	.002	.068	.795
Explained	10.479	15	.699	20.594	.000
Residual	2.714	80	.034		
Total	13.192	95	.139		

Table X. Analysis of variance for the plot volume index of pine seedlings.

Source of variation	SS	DF	MS	F	Fpr
Main effects	32648.410	4	8162.103	64.761	.000
AR	1214.830	1	1212.830	9.639	.003
D	920.481	1	920.481	7.303	.008
ST	30506.010	1	30506.010	242.045	.000
PR	303.011	1	303.011	2.404	.125
2-way interactions	2312.388	6	385.398	3.058	.010
AR D	105.369	1	105.369	.836	.363
AR ST	395.766	1	395.766	3.140	.080
AR PR	488.086	1	488.086	3.873	.053
D ST	34.425	1	34.425	.273	.603
D PR	169.911	1	169.911	1.348	.249
ST PR	1185.121	1	1185.121	9.403	.003
3-way interactions	432.208	4	108.052	.857	.493
AR D ST	7.691	1	7.691	.061	.806
AR D PR	15.729	1	15.729	.125	.725
AR ST PR	343.967	1	343.967	2.729	.102
D ST PR	84.477	1	84.477	.670	.415
4-way interactions	43.877	1	43.877	.348	.557
AR D ST PR	43.877	1	43.877	.348	.557
Explained	35436.884	15	2362.459	18.745	.000
Residual	10082.754	80	126.034		
Total	45519.638	95	479.154		

Table XI. Analysis of variance for pine dry weight.

	Aboveground dry weight					Belowground dry weight				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	37.081	4	9.270	70.431	.000	17.990	4	4.497	66.012	.000
AR	3.167	1	3.167	24.063	.000	.047	1	.047	.687	.410
D	.543	1	.543	4.122	.046	.022	1	.022	.322	.572
ST	32.191	1	32.191	244.572	.000	17.061	1	17.061	250.426	.000
PR	1.180	1	1.180	8.968	.004	.859	1	.859	12.614	.001
2-way interactions	4.580	6	.763	5.799	.000	1.460	6	.243	3.571	.003
AR D	.494	1	.494	3.754	.056	.003	1	.003	.049	.825
AR ST	1.028	1	1.028	7.808	.007	.001	1	.001	.019	.891
AR PR	.050	1	.050	.382	.538	.140	1	.140	2.054	.156
D ST	.017	1	.017	.130	.720	.013	1	.013	.189	.665
D PR	.362	1	.362	2.750	.101	.014	1	.014	.201	.655
ST PR	2.628	1	2.628	19.970	.000	1.289	1	1.289	18.916	.000
3-way interactions	1.424	4	.356	2.704	.036	.355	4	.084	1.231	.304
AR D ST	.291	2	.291	2.209	.141	.012	1	.012	.182	.671
AR D PR	.675	1	.675	5.127	.026	.203	1	.203	2.975	.088
AR ST PR	.007	1	.007	.056	.814	.097	1	.097	1.421	.237
D ST PR	.451	1	.451	3.425	.068	.024	1	.024	.345	.558
4-way interactions	.180	1	.180	1.370	.245	.076	1	.076	1.117	.294
AR D ST PR	.180	1	.180	1.370	.245	.076	1	.076	1.117	.294
Explained	43.265	15	2.884	21.914	.000	19.861	15	1.324	19.435	.000
Residual	10.530	80	.132			5.450	80	.068		
Total	53.795	95	.566			25.311	95	.266		

Table XII. Analysis of variance for the root surface area of pine seedlings.

Source of variation	SS	DF	MS	F	Fpr
Main effects	1860179.829	4	465044.957	94.049	.000
AR	9627.643	1	9627.643	1.947	.167
D	6407.617	1	6407.617	1.296	.258
ST	1755160.062	1	1755160.062	354.957	.000
PR	74460.382	1	74460.382	15.059	.000
2-way interactions	119173.671	6	19862.278	4.017	.001
AR D	1711.967	1	1711.967	.346	.558
AR ST	1568.712	1	1568.712	.317	.575
AR PR	11282.348	1	11282.348	2.282	.135
D ST	9.784	1	9.784	.002	.965
D PR	949.642	1	949.642	.192	.662
ST PR	81036.285	1	81036.285	16.388	.000
3-way interactions	24706.766	4	6176.692	1.249	.297
AR D ST	5329.867	1	5329.867	1.078	.302
AR D PR	604.210	1	604.210	.122	.728
AR ST PR	11712.800	1	11712.800	2.369	.128
D ST PR	8.537	1	8.537	.002	.967
Explained	2004060.266	14	143147.162	28.950	.000
Residual	400521.788	81	4944.713		
Total	2404582.054	95	25311.390		

Table XIII. Analysis of variance for the shoot : root ratio of pine seedlings.

Source of variation	SS	DF	MS	F	Fpr
Main effects	28.394	4	7.099	13.727	.000
AR	4.914	1	4.914	9.503	.003
D	.175	1	.175	.339	.562
ST	23.305	1	23.305	45.067	.000
PR	.000	1	.000	.000	.000
2-way interactions	3.128	6	.521	1.008	.426
AR D	2.112	1	2.112	4.085	.047
AR ST	.350	1	.350	.678	.413
AR PR	.313	1	.313	.605	.439
D ST	.168	1	.168	.326	.570
D PR	.022	1	.022	.043	.836
ST PR	.162	1	.162	.313	.578
3-way interactions	2.168	4	.542	1.048	.388
AR D ST	.002	1	.002	.005	.946
AR D PR	.109	1	.109	.211	.647
AR ST PR	1.643	1	1.643	3.178	.078
D ST PR	.413	1	.413	.800	.374
4-way interactions	.135	1	.135	.261	.611
AR D ST PR	.135	1	.135	.261	.611
Explained	33.826	15	2.255	4.361	.000
Residual	41.369	80	.517		
Total	75.195	95	.792		

Table. XIV. Analysis of variance for the water saturation deficit of pine seedlings.

Time	Nov 2					Nov 7				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	232.731	4	58.183	12.090	.000	7825.918	4	1956.480	270.915	.000
AR	9.845	1	9.845	2.046	.157	413.836	1	413.836	57.304	.000
D	216.746	1	216.764	45.041	.000	7093.555	1	7093.555	982.249	.000
ST	.147	1	.147	.031	.862	125.390	1	125.390	17.363	.000
PR	2.638	1	2.638	.548	.461	58.434	1	58.434	8.091	.006
2-way interactions	25.179	6	4.197	.872	.519	460.831	6	76.805	10.635	.000
AR D	9.107	1	9.107	1.892	.173	222.947	1	222.947	30.872	.000
AR ST	1.632	1	1.632	.339	.562	41.131	1	41.131	5.695	.019
AR PR	.977	1	.977	.203	.654	7.252	1	7.252	1.004	.319
D ST	2.451	1	2.451	.509	.478	140.224	1	140.224	19.417	.000
D PR	.275	1	.275	.057	.812	64.655	1	64.655	8.953	.000
ST PR	11.894	1	11.894	2.472	.120	14.082	1	14.082	1.950	.167
3-way interactions	7.304	4	1.826	.379	.823	3.759	4	.940	.130	.971
AR D ST	4.305	1	4.305	.895	.347	.169	1	.169	.023	.879
AR D PR	2.139	1	2.139	.444	.507	2.297	1	2.297	.318	.574
AR ST PR	.004	1	.004	.001	.976	1.194	1	1.194	.165	.685
D ST PR	.692	1	.692	.144	.706	.013	1	.013	.002	.967
4-way interactions	3.448	1	3.448	.716	.400	2.517	1	2.517	.349	.557
AR D ST PR	3.448	1	3.448	.716	.400	2.517	1	2.517	.349	.557
Explained	268.662	15	17.911	3.722	.000	8293.025	15	552.868	76.556	.000
Residual	375.380	78	4.813			563.296	78	7.222		
Total	644.042	93	6.925			8856.322	93	95.229		

Table XV. Analysis of variance for the fluorescence parameters of pine seedlings.

Parameters	Fv					Fv/Fm					1/2t				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Main effects	6.495	6	1.082	36.434	.000	2.120	6	.353	26.803	.000	174364.639	6	29060.773	23.340	.000
Day	5.865	2	2.932	98.694	.000	1.572	2	.786	59.630	.000	131090.333	2	65545.167	52.641	.000
AR	.001	1	.001	.028	.867	.028	1	.028	2.130	.146	13448.000	1	13448.000	10.800	.001
D	.095	1	.095	3.197	.075	.136	1	.136	10.333	.001	6555.125	1	6555.125	5.265	.023
ST	.533	1	.533	17.941	.000	.382	1	.382	28.989	.000	23256.056	1	23256.056	18.678	.000
PR	.001	1	.001	.049	.824	.001	1	.001	.107	.744	15.125	1	15.125	.012	.912
2-way interactions	.820	14	.059	1.971	.021	.356	14	.025	1.931	.024	25695.694	14	1835.407	1.474	.121
Day AR	.002	2	.002	.030	.971	.015	2	.007	.552	.576	2241.083	2	1120.542	.900	.408
Day D	.012	2	.006	.199	.820	.020	2	.010	.773	.463	4599.250	2	2299.625	1.847	.160
Day ST	.049	2	.025	.829	.438	.015	2	.008	.571	.566	2504.111	2	1252.056	1.006	.367
Day PR	.065	2	.033	1.102	.334	.031	2	.016	1.180	.309	4505.083	2	2252.542	1.809	.166
AR D	.023	1	.023	.760	.384	.011	1	.011	.803	.371	19.014	1	19.014	.015	.902
AR ST	.144	1	.144	4.862	.028	.078	1	.078	5.942	.016	953.389	1	953.389	.766	.382
AR PR	.005	1	.005	.171	.679	.000	1	.000	.001	.980	9135.014	1	9135.014	7.337	.007
D ST	.436	1	.436	14.686	.000	.178	1	.178	13.508	.000	1128.125	1	1128.125	.908	.342
D PR	.015	1	.015	.501	.480	.000	1	.000	.009	.924	544.500	1	544.500	.437	.509
ST PR	.068	1	.068	2.294	.131	.008	1	.008	.620	.432	66.125	1	66.125	.053	.818
3-way interactions	.284	16	.018	.598	.884	.238	16	.015	1.127	.330	12977.944	16	811.122	.651	.839
Day AR D	.008	2	.004	.129	.879	.009	2	.005	.355	.701	1553.694	2	776.847	.624	.537
Day AR ST	.022	2	.011	.368	.693	.046	2	.023	1.763	.174	607.194	2	303.597	.244	.784
Day AR PR	.011	2	.006	.187	.829	.008	2	.004	.301	.740	1204.528	2	602.264	.484	.617
Day D ST	.048	2	.024	.800	.451	.032	2	.016	1.206	.301	805.083	2	402.542	.323	.724
Day D PR	.039	2	.020	.659	.518	.025	2	.013	.958	.385	1521.000	2	760.500	.611	.544
Day ST PR	.125	2	.063	2.111	.123	.044	2	.022	1.664	.192	638.083	2	319.042	.256	.744

Table XV, cont.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AR D ST	.015	1	.015	2.111	.123	.039	1	.039	2.924	.089	4035.014	1	4035.014	3.241	.073
AR D PR	.006	1	.006	.213	.645	.031	1	.031	2.314	.130	1058.000	1	1058.000	.850	.358
AR ST PR	.008	1	.008	.281	.597	.003	1	.003	.227	.634	203.347	1	203.347	.163	.686
D ST PR	.002	1	.002	.081	.777	.001	1	.001	.079	.779	1352.000	1	1352.000	1.086	.298
4-way interactions	.162	9	.018	.605	.793	.113	9	.013	.951	.481	12188.861	9	1354.318	1.088	.372
Day AR D ST	.051	2	.026	.866	.422	.021	2	.010	.782	.459	3276.361	2	1638.181	1.316	.270
Day AR D PR	.067	2	.033	1.124	.327	.013	2	.007	.499	.608	255.083	2	127.542	.102	.903
Day AR ST PR	.013	2	.006	.217	.805	.027	2	.014	1.031	.358	1702.694	2	851.347	.684	.506
Day D ST PR	.029	2	.014	.487	.615	.001	2	.001	.041	.960	6821.333	2	3410.667	2.739	.067
AR D ST PR	.002	1	.002	.056	.814	.051	1	.051	3.855	.051	133.389	1	133.389	.107	.744
5-way interactions	.050	2	.025	.835	.435	.012	2	.006	.455	.635	4600.194	2	2300.097	1.847	.160
Day AR D ST PR	.050	2	.025	.835	.435	.012	2	.006	.455	.635	4600.194	2	2300.097	1.847	.160
Explained	7.810	47	.166	5.593	.000	2.840	47	.060	4.582	.000	229827.333	47	4889.943	3.927	.000
Residual	7.131	240	.030			3.164	240	.013			298830.667	240	1245.128		
Total	14.941	287	.052			6.004	287	.021			528658.000	287	1842.014		

Table XVI. Analysis of variance for poplar height.

Time	Aug 18					Sept 20					Nov 11				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	2488.021	4	622.005	12.907	.000	8314.072	4	2078.518	23.183	.000	20791.406	4	5197.852	30.916	.000
AR	126.042	1	126.042	2.615	.110	110.082	1	110.082	1.228	.271	745.378	1	745.378	4.433	.038
D	38.760	1	38.760	.804	.373	190.407	1	190.407	2.127	.149	796.378	1	796.378	4.737	.032
ST	459.375	1	459.375	9.532	.003	3980.950	1	3980.950	44.402	.000	10055.273	1	10055.273	59.807	.000
PR	1863.844	1	1863.844	38.675	.000	4032.634	1	4032.634	44.979	.000	9194.378	1	9194.378	54.687	.000
2-way interactions	137.896	6	22.983	.477	.824	610.493	6	101.749	1.135	.350	1353.724	6	225.621	1.342	.248
AR D	77.042	1	77.042	1.599	.210	34.082	1	34.082	.380	.539	95.003	1	95.003	.565	.454
AR ST	.010	1	.010	.000	.988	.350	1	.350	.004	.950	251.878	1	251.878	1.498	.225
AR PR	6.000	1	6.000	.125	.725	39.270	1	39.270	.438	.510	217.503	1	217.503	1.294	.259
D ST	.042	1	.042	.001	.977	329.300	1	329.300	3.673	.059	612.565	1	612.565	3.643	.060
D PR	3.760	1	3.760	.078	.781	87.784	1	87.784	.979	.325	25.523	1	25.523	.152	.698
ST PR	51.042	1	51.042	1.059	.307	119.707	1	119.707	1.335	.251	151.253	1	151.253	.900	.346
3-way interactions	97.062	4	24.266	.504	.733	183.754	4	45.939	.512	.727	314.156	4	78.539	.467	.760
AR D ST	5.510	1	5.510	.114	.736	80.300	1	80.300	.896	.347	172.003	1	172.003	1.023	.315
AR D PR	48.167	1	48.167	.999	.320	34.320	1	34.320	.383	.538	127.190	1	127.190	.757	.387
AR ST PR	41.344	1	41.344	.858	.357	45.927	1	45.927	.512	.476	5.273	1	5.273	.031	.860
D ST PR	2.042	1	2.042	.042	.837	23.207	1	23.207	.259	.612	9.690	1	9.690	.058	.811
4-way interactions	178.760	1	178.760	3.709	.058	466.402	1	466.402	5.202	.025	122.628	1	122.628	.729	.396
AR D ST PR	178.760	1	178.760	3.709	.058	466.402	1	466.402	5.202	.025	122.628	1	122.628	.729	.396
Explained	2901.740	15	193.449	4.014	.000	9574.722	15	638.315	7.120	.000	22581.914	15	1505.461	8.954	.000
Residual	3855.417	80	48.193			7172.517	80	89.656			13450.208	80	168.128		
Total	6757.156	95	71.128			16747.238	95	176.287			36032.122	95	379.285		

Table XVII. Analysis of variance for poplar stem diameter.

Source of variation	SS	DF	MS	F	Fpr
Main effects	90.114	4	22.528	12.889	.000
AR	.397	1	.397	.227	.635
D	8.455	1	8.455	4.837	.031
ST	61.488	1	61.488	35.178	.000
PR	19.774	1	19.744	11.313	.001
2-way interactions	4.536	6	.756	.433	.855
AR D	.001	1	.001	.000	.983
AR ST	2.805	1	2.805	1.605	.209
AR PR	.118	1	.118	.068	.795
D ST	.253	1	.253	.145	.705
D PR	.128	1	.128	.073	.787
ST PR	1.231	1	1.231	.704	.404
3-way interactions	2.802	4	.700	.401	.808
AR D ST	.776	1	.776	.444	.507
AR D PR	.379	1	.379	.217	.643
AR ST PR	1.615	1	1.615	.924	.339
D ST PR	.033	1	.033	.019	.892
4-way interactions	3.326	1	3.326	1.903	.172
AR D ST PR	3.326	1	3.326	1.903	.172
Explained	100.779	15	6.719	3.844	.000
Residual	139.833	80	1.748		
Total	240.611	95			

Table XVIII. Analysis of variance for poplar dry weight.

	Aboveground					Belowground				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	334.529	4	83.632	21.268	.000	80.535	4	20.134	7.875	.000
AR	12.885	1	12.885	3.277	.074	9.891	1	9.891	3.869	.053
D	72.136	1	72.136	18.345	.000	14.442	1	14.442	5.649	.020
ST	216.465	1	216.465	55.048	.000	56.030	1	56.030	21.915	.000
PR	33.042	1	33.042	8.403	.005	.171	1	.171	.067	.797
2-way interactions	21.201	6	3.534	.899	.500	15.019	6	2.503	.979	.445
AR D	4.413	1	4.413	1.122	.293	.061	1	.061	.024	.878
AR ST	.013	1	.013	.003	.954	5.415	1	5.415	2.118	.149
AR PR	.259	1	.259	.066	.798	1.798	1	1.798	.703	.404
D ST	15.636	1	15.636	3.976	.050	2.085	1	2.085	.816	.369
D PR	.612	1	.612	.156	.694	.848	1	.848	.332	.566
ST PR	.268	1	.268	.068	.795	4.811	1	4.811	1.882	.174
3-way interactions	3.105	4	.776	.197	.939	2.039	4	.510	.199	.938
AR D ST	.304	1	.304	.077	.782	.135	1	.135	.053	.819
AR D PR	1.176	1	1.176	.299	.586	.083	1	.083	.032	.857
AR ST PR	.520	1	.520	.132	.717	.001	1	.001	.000	.985
D ST PR	1.105	1	1.105	.281	.597	1.820	1	1.820	.712	.401
4-way interactions	1.875	1	1.875	.477	.492	2.254	1	2.254	.882	.351
AR D ST PR	1.875	1	1.875	.477	.492	2.254	1	2.254	.882	.351
Explained	360.711	15	24.047	6.115	.000	99.847	15	6.656	2.604	.003
Residual	314.582	80	3.932			204.537	80	2.557		
Total	675.293	95	7.108			304.383	95			

Table XIX. Analysis of variance for the root surface area of poplar cuttings.

Source of variation	SS	DF	MS	F	Fpr
Main effects	1448637.054	4	362159.263	10.946	.000
AR	102312.246	1	102312.246	3.092	.082
D	198136.241	1	198136.241	5.988	.017
ST	1091640.934	1	1091640.934	32.994	.000
PR	43042.895	1	43042.895	1.301	.257
2-way interactions	251650.114	6	41941.686	1.268	.282
AR D	4669.058	1	4669.058	.141	.708
AR ST	66987.819	1	66987.819	2.025	.159
AR PR	3600.909	1	3600.909	.109	.742
D ST	25631.415	1	25631.415	.775	.381
D PR	5009.773	1	5009.773	.151	.698
ST PR	115500.022	1	115500.022	3.491	.065
3-way interactions	55133.827	4	13783.457	.417	.796
AR D ST	1896.562	1	1896.562	.057	.811
AR D PR	15346.762	1	15346.762	.464	.498
AR ST PR	611.692	1	611.692	.018	.892
D ST PR	42194.360	1	42194.360	1.275	.262
Explained	1755420.995	14	125387.214	3.790	.000
Residual	2679990.277	81	33086.300		
Total	4435411.271	95	46688.540		

Table XX. Analysis of variance for the shoot : root ratio in poplar cuttings.

Source of variation	SS	DF	MS	F	Fpr
Main effects	54.739	4	13.685	8.729	.000
AR	29.826	1	26.829	19.026	.000
D	5.297	1	5.297	3.379	.070
ST	12.262	1	12.262	7.822	.006
PR	7.354	1	7.354	4.691	.033
2-way interactions	11.371	6	1.895	1.209	.310
AR D	1.987	1	1.987	1.267	.264
AR ST	3.349	1	3.349	2.136	.148
AR PR	.761	1	.761	.486	.488
D ST	2.139	1	2.139	1.364	.264
D PR	.622	1	.622	.397	.530
ST PR	2.512	1	2.512	1.603	.209
3-way interactions	3.838	4	.959	.612	.655
AR D ST	1.258	1	1.258	.803	.373
AR D PR	.022	1	.022	.014	.906
AR ST PR	.865	1	.865	.551	.460
D ST PR	1.693	1	1.693	1.080	.302
4-way interactions	.450	1	.450	.287	.594
AR D ST PR	.450	1	.450	.287	.594
Explained	70.397	15	4.693	2.994	.001
Residual	125.416	80	1.568		
Total	195.813	95	2.061		

Table XXI. Analysis of variance for the water saturation deficit of poplar cuttings.

Time	Nov 2					Nov 7				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
Main effects	79.968	4	19.992	1.869	.124	3189.894	4	797.474	35.654	.000
AR	2.638	1	2.638	.247	.621	32.791	1	32.791	1.466	.230
D	54.780	1	54.780	5.122	.026	3067.621	1	3067.621	137.149	.000
ST	8.190	1	8.190	.766	.384	3.166	1	3.166	.142	.708
PR	12.688	1	12.688	1.186	.279	49.335	1	49.335	2.206	.142
2-way interactions	18.029	6	3.005	.281	.944	104.548	6	17.425	.779	.589
AR D	3.112	1	3.112	.291	.591	16.764	1	16.764	.750	.389
AR ST	6.728	1	6.728	.629	.430	.770	1	.770	.034	.853
AR PR	1.215	1	1.215	.114	.737	29.384	1	29.384	1.314	.255
D ST	.004	1	.004	.000	.984	.029	1	.029	.001	.971
D PR	.337	1	.337	.032	.860	2.220	1	2.220	.099	.754
ST PR	6.160	1	6.160	.576	.450	53.495	1	53.495	2.392	.126
3-way interactions	16.303	4	16.303	4.076	.822	35.861	4	8.965	.401	.807
AR D ST	13.644	1	13.644	1.276	.262	26.472	1	26.472	1.184	.280
AR D PR	.000	1	.000	.000	.996	9.460	1	9.460	.423	.517
AR ST PR	.042	1	.042	.004	.950	.418	1	.418	.019	.892
D ST PR	2.246	1	2.246	.210	.648	.191	1	.191	.009	.927
4-way interactions	6.695	1	6.695	.626	.431	5.073	1	5.073	.227	.635
AR D ST PR	6.695	1	6.695	.626	.431	5.073	1	5.073	.227	.635
Explained	120.995	15	8.066	.754	.722	3335.376	15	222.358	9.941	.000
Residual	834.192	78	10.695			1744.637	78	22.367		
Total	955.187	93				5080.013	93			

Table XXII. Analysis of variance for the transpiration rates in poplar cuttings.

Time	September					November				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11
Main effects	822.380	9	91.376	10.344	.000	744.332	9	82.704	19.944	.000
Day	361.180	5	72.236	8.177	.000	634.400	5	126.880	30.597	.000
AR	19.884	1	19.884	2.251	.135	32.498	1	32.498	7.837	.006
D	398.835	1	398.835	45.150	.000	33.134	1	33.134	7.990	.005
ST	37.324	1	37.324	4.225	.041	31.303	1	31.303	7.549	.007
PR	3.308	1	3.308	.374	.541	12.862	1	12.862	3.102	.080
2-way interactions	461.527	26	17.751	2.009	.004	578.038	26	22.232	5.361	.000
Day AR	56.531	5	11.306	1.280	.274	31.373	5	6.275	1.513	.187
Day D	277.092	5	55.418	6.274	.000	472.979	5	94.596	22.812	.000
Day ST	28.872	5	5.774	.654	.659	31.690	5	6.338	1.528	.183
Day PR	43.711	5	8.742	.990	.425	29.107	5	5.821	1.404	.225
AR D	20.560	1	20.560	2.327	.129	8.848	1	8.848	2.134	.146
AR ST	15.300	1	15.300	1.732	.190	.133	1	.133	.032	.858
AR PR	.878	1	.878	.099	.753	.836	1	.836	.202	.654
D ST	5.220	1	5.220	.591	.443	.602	1	.602	.145	.704
D PR	4.698	1	4.698	.532	.467	.526	1	.526	.127	.722
ST PR	8.025	1	8.025	.908	.342	.840	1	.840	.203	.653
3-way interactions	244.104	34	7.180	.813	.760	110.781	34	3.258	.786	.796
Day AR D	53.305	5	10.661	1.207	.307	12.222	5	2.444	.589	.708
Day AR ST	15.363	5	3.073	.348	.883	6.665	5	1.333	.321	.900
Day AR PR	43.526	5	8.705	.985	.428	16.596	5	3.319	.800	.551
Day D ST	22.483	5	4.497	.509	.769	17.423	5	3.485	.840	.523
Day D PR	47.982	5	9.596	1.086	.369	31.732	5	6.346	1.530	.182
Day ST PR	29.445	5	5.889	.667	.649	5.441	5	1.088	.262	.933

Table XXII, cont.

1	2	3	4	5	6	7	8	9	10	11
AR D ST	10.579	1	10.579	1.198	.275	16.292	1	16.292	3.929	.049
AR D PR	2.796	1	2.796	.317	.574	.037	1	.037	.009	.925
AR ST PR	5.035	1	5.035	.570	.451	4.062	1	4.062	.979	.324
D ST PR	12.897	1	12.897	1.460	.228	.199	1	.199	.048	.827
4-way interactions	125.325	21	5.968	.676	.854	102.527	21	4.882	1.177	.275
Day AR D ST	14.531	5	2.906	.329	.895	16.781	5	3.356	.809	.544
Day AR D PR	43.287	5	8.657	.980	.431	36.378	5	7.276	1.754	.124
Day AR ST PR	31.377	5	6.275	.710	.616	4.708	5	.942	.227	.950
Day D ST PR	29.809	5	5.962	.675	.643	20.284	5	4.057	.978	.432
AR D ST PR	8.073	1	8.073	.914	.340	24.632	1	24.632	5.940	.016
5-way interactions	28.107	5	5.621	.636	.672	9.417	5	1.883	.454	.810
Day AR D ST PR	28.107	5	5.621	.636	.672	9.417	5	1.183	.454	.810
Explained	1681.443	95	17.699	2.004	.000	1545.095	95	16.264	3.922	.000
Residual	1696.048	192	8.834			796.189	192	4.147		
Total	3377.491	287	11.768			2341.284	287	8.158		

Table XXIII. Analysis of variance for the diffusive resistance in poplar cuttings.

Time	September					November				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11
Main effects	22837.076	9	2537.453	67.250	.000	1385.421	9	153.936	43.807	.000
Day	8774.542	5	1754.908	46.510	.000	910.053	5	182.011	51.796	.000
AR	1.444	1	1.444	.038	.845	9.985	1	9.985	2.841	.093
D	11726.418	1	11726.418	310.785	.000	459.982	1	459.982	130.901	.000
ST	2323.265	1	2323.265	61.573	.000	2.656	1	2.656	.756	.386
PR	5.839	1	5.839	.155	.694	.007	1	.007	.002	.965
2-way interactions	2937.566	26	112.983	2.994	.000	983.039	26	37.809	10.760	.000
Day AR	169.457	5	33.891	.898	.483	6.704	5	1.341	.382	.861
Day D	2029.106	5	405.821	10.755	.000	904.337	5	180.867	51.471	.000
Day ST	189.290	5	37.858	1.003	.417	5.969	5	1.194	.340	.888
Day PR	25.497	5	5.099	.135	.984	18.269	5	3.654	1.040	.396
AR D	.889	1	.889	.024	.878	7.176	1	7.176	2.042	.155
AR ST	2.560	1	2.560	.068	.795	.108	1	.108	.031	.861
AR PR	18.949	1	18.949	.502	.479	3.473	1	3.473	.988	.321
D ST	494.825	1	494.825	13.114	.000	1.770	1	1.770	.504	.479
D PR	3.181	1	3.181	.084	.772	18.234	1	18.234	5.189	.024
ST PR	.201	1	.201	.005	.942	13.636	1	13.636	3.881	.050
3-way interactions	768.461	34	22.602	.599	.961	96.819	34	2.848	.810	.763
Day AR D	31.208	5	6.242	.165	.975	18.216	5	3.643	1.037	.397
Day AR ST	30.518	5	6.104	.162	.976	3.865	5	.773	.220	.954
Day AR PR	129.013	5	25.803	.684	.636	3.999	5	.800	.228	.950
Day D ST	87.667	5	17.533	.465	.802	12.087	5	2.417	.688	.633
Day D PR	61.574	5	12.315	.326	.897	28.173	5	5.635	1.604	.161
Day ST PR	209.292	5	41.858	1.109	.357	17.718	5	3.544	1.008	.414

Table XXIII, cont.

1	2	3	4	5	6	7	8	9	10	11
AR D ST	18.353	1	18.353	.486	.486	.062	1	.062	.018	.894
AR D PR	80.052	1	80.052	2.122	.147	.020	1	.020	.006	.940
AR ST PR	68.863	1	68.863	1.825	.178	1.528	1	1.528	.435	.510
D ST PR	54.930	1	54.930	1.456	.229	10.453	1	10.453	2.975	.086
4-way interactions	355.164	21	16.913	.448	.983	62.096	21	2.957	.841	.666
Day AR D ST	56.950	5	11.390	.302	.911	1.878	5	.376	.107	.991
Day AR D PR	91.709	5	18.342	.486	.786	17.346	5	3.469	.987	.427
Day AR ST PR	142.001	5	28.400	.753	.585	1.163	5	.233	.066	.997
Day D ST PR	50.953	5	10.191	.270	.929	26.215	5	5.243	1.492	.194
AR D ST PR	15.721	1	15.721	.417	.519	15.406	1	15.406	4.384	.038
5-way interactions	96.726	5	19.345	.513	.766	5.238	5	1.048	.268	.913
Day AR D ST PR	96.726	5	19.345	.513	.766	5.238	5	1.048	.268	.913
Explained	26994.993	95	284.158	7.531	.000	2532.613	95	26.659	7.587	.000
Residual	7244.467	192	37.732			674.681	192	3.514		
Total	34239.460	287	119.301			3207.294	287	11.175		

Table XXIV. Analysis of variance for the fluorescence parameters in poplar cuttings.

Parameters	Fv					Fv/Fm					1/2 t				
Source of variation	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr	SS	DF	MS	F	Fpr
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Main effects	8.080	6	1.347	22.011	.000	2.011	6	.335	6.558	.000	109593.424	6	18265.571	10.014	.000
Day	7.461	2	3.730	60.974	.000	.386	2	.193	3.772	.024	54546.549	2	27273.274	14.953	.000
AR	.013	1	.013	.216	.643	.020	1	.020	.390	.533	2432.531	1	2432.531	1.334	.249
D	.112	1	.112	1.837	.177	.058	1	.058	1.128	.289	621.281	1	621.281	.341	.560
ST	.169	1	.169	2.757	.098	.140	1	.140	2.730	.100	552.781	1	552.781	.303	.582
PR	.325	1	.325	5.307	.022	1.408	1	1.408	27.557	.000	51440.281	1	51440.281	28.202	.000
2-way interactions	.647	14	.046	.756	.717	.418	14	.030	.585	.876	12234.868	14	873.919	.479	.943
Day AR	.023	2	.011	.187	.829	.000	2	.000	.001	.999	702.438	2	351.219	.193	.825
Day D	.048	2	.024	.391	.677	.001	2	.000	.009	.991	819.438	2	409.719	.225	.799
Day ST	.026	2	.013	.212	.809	.001	2	.000	.009	.991	650.271	2	325.135	.178	.837
Day PR	.075	2	.037	.609	.545	.005	2	.002	.047	.954	764.312	2	382.156	.210	.811
AR D	.010	1	.010	.158	.691	.013	1	.013	.263	.608	693.781	1	693.781	.380	.538
AR ST	.241	1	.241	3.938	.048	.222	1	.222	4.341	.038	3894.031	1	3894.031	2.135	.145
AR PR	.023	1	.023	.375	.541	.014	1	.014	.281	.597	514.670	1	514.670	.282	.596
D ST	.035	1	.035	.570	.451	.025	1	.025	.494	.483	4012.587	1	4012.587	2.200	.139
D PR	.028	1	.028	.461	.498	.012	1	.012	.237	.627	154.587	1	154.587	.087	.771
ST PR	.139	1	.139	2.274	.133	.125	1	.125	2.439	.120	28.753	1	28.753	.016	.900
3-way interactions	.397	16	.025	.405	.980	.247	16	.015	2.302	.996	22384.208	16	1399.013	.767	.722
Day AR D	.032	2	.016	.264	.768	.000	2	.000	.001	.999	106.021	2	53.010	.029	.971
Day AR ST	.061	2	.031	.502	.606	.001	2	.001	.014	.986	1567.521	2	783.760	.430	.651
Day AR PR	.010	2	.005	.080	.923	.001	2	.001	.012	.989	869.674	2	434.837	.238	.788
Day D ST	.089	2	.045	.728	.484	.005	2	.003	.049	.952	2127.799	2	1063.899	.583	.559
Day D PR	.007	2	.003	.057	.945	.000	2	.000	.000	1.000	1207.840	2	603.920	.331	.718
Day ST PR	.192	2	.096	1.572	.210	.025	2	.013	.245	.783	884.090	2	442.045	.242	.785

Table XXIV, cont.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AR D ST	.001	1	.001	.011	.915	.014	1	.014	.281	.596	270.281	1	270.281	.148	.701
AR D PR	.004	1	.004	.067	.795	.011	1	.011	.220	.639	166.531	1	166.531	.091	.763
AR ST PR	.000	1	.000	.000	.998	.166	1	.166	3.251	.073	12786.670	1	12786.670	7.010	.009
D ST PR	.000	1	.000	.000	.994	.022	1	.022	.435	.510	2397.781	1	2397.781	1.315	.253
4-way interactions	.089	9	.010	.161	.997	.019	9	.002	.042	1.000	4289.406	9	476.601	.261	.984
Day AR D ST	.021	2	.010	.171	.843	.007	2	.004	.073	.930	256.688	2	128.344	.070	.932
Day AR D PR	.021	2	.011	.172	.842	.001	2	.000	.005	.995	467.896	2	233.948	.128	.880
Day AR ST PR	.020	2	.010	.159	.853	.001	2	.000	.010	.991	1656.757	2	828.378	.454	.636
Day D ST PR	.014	2	.007	.114	.892	.000	2	.000	.004	.996	52.646	2	26.323	.014	.986
AR D ST PR	.013	1	.013	.220	.639	.010	1	.010	.198	.657	1855.420	1	1855.420	1.017	.314
5-way interactions	.050	2	.025	.410	.664	.004	2	.002	.040	.961	435.507	2	217.753	.119	.888
Day AR D ST PR	.050	2	.025	.410	.664	.004	2	.002	.040	.961	435.507	2	217.753	.119	.888
Explained	9.263	47	.197	3.221	.000	2.700	47	.057	1.124	.283	148937.413	47	3168.881	1.737	.004
Residual	14.683	240	.061			12.265	240	.051			437756.833	240	1823.987		
Total	23.946	287	.083			14.964	287	.052			586694.247	287	2044.231		

APPENDIX II

Table I. Pine mean height, cm.

	Treatments	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Day	drought	control	drought	control	drought	control	drought	control
Northern	Aug 18	3.88	3.98	3.75	3.45	5.80	6.17	5.20	5.43
	Sept 20	4.25	4.60	4.13	3.93	6.60	6.82	5.75	5.95
	Nov 11	4.58	4.95	4.27	4.33	7.68	8.03	6.07	7.00
Southern	Aug 18	3.62	3.78	3.55	3.55	6.43	5.68	6.35	6.65
	Sept 20	3.83	4.28	3.82	3.83	7.20	6.47	6.68	7.07
	Nov 11	4.05	4.80	4.00	3.97	7.58	9.15	7.32	7.60

Table II. Pine mean water saturation deficit, %.

	Treatments	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Day	drought	control	drought	control	drought	control	drought	control
Northern	Nov 2	8.07	5.93	9.18	5.06	6.94	5.00	8.50	4.81
	Nov 7	21.70	6.30	27.04	5.65	14.85	5.19	23.18	5.92
Southern	Nov 2	7.64	5.07	9.31	4.38	8.38	5.20	8.96	6.73
	Nov 7	23.60	4.94	29.62	4.87	18.52	4.23	27.17	7.81

Table III. Poplar mean height, cm.

	Treatments	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Day	drought	control	drought	control	drought	control	drought	control
	Aug 18	7.00	9.17	11.08	6.08	15.00	10.25	15.25	16.17
Northern	Sept 20	10.05	12.08	13.50	7.83	27.42	22.42	20.92	33.17
	Nov 11	11.42	15.08	16.25	10.67	36.42	41.58	25.83	41.50
	Aug 18	16.67	16.42	21.75	19.58	18.33	23.25	25.25	19.25
Southern	Sept 20	24.87	22.33	27.22	29.83	29.75	41.75	34.25	41.08
	Nov 11	34.33	41.42	34.17	31.83	52.00	67.08	43.58	50.92

Table IV. Poplar mean water saturation deficit, %.

	Treatments	Heavy soil				Light soil			
		pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Provenance	Day	drought	control	drought	control	drought	control	drought	control
Northern	Nov 2	6.86	6.53	7.36	3.72	7.14	4.91	6.25	5.85
	Nov 7	15.01	5.70	18.51	3.65	17.29	4.92	19.92	6.64
Southern	Nov 2	7.92	7.40	7.91	6.27	6.86	5.28	7.37	5.52
	Nov 7	16.96	7.13	21.25	7.25	15.49	4.77	18.74	6.19

Table V. Mean transpiration rates (μg/cm /s) and diffusive resistance (s/cm) in poplar cuttings at the begining of the treatment period.

		Treatments	Heavy soil				Light soil			
			pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Day	Parameters	Provenance	drought	control	drought	control	drought	control	drought	control
Sept 21	Tr. rate		21.050	26.860	19.980	23.810	37.500	37.600	26.490	36.140
	D. res.		0.460	0.992	0.497	0.351	0.180	0.145	0.293	0.250
Sept 21	Tr. rate		11.680	16.700	10.443	19.530	17.886	26.573	12.837	23.380
	D. res.		0.850	0.481	0.992	0.544	0.590	0.338	0.612	0.330
Sept 23	Tr. rate	Northern	6.758	18.826	5.592	17.671	7.737	25.325	7.296	23.543
	D. res.		2.013	1.611	2.490	0.827	1.805	0.380	1.760	0.344
Sept 24	Tr. rate		4.957	17.267	5.177	17.241	6.909	27.988	7.460	24.845
	D. res.		3.610	0.510	4.150	1.700	2.790	0.417	2.090	0.340
Sept 25	Tr. rate		2.356	14.435	3.064	18.475	4.217	19.685	5.085	25.532
	D. res.		2.609	0.712	3.860	0.740	11.653	0.640	2.185	0.300
Sept 26	Tr. rate		1.834	15.373	1.608	18.422	4.693	21.953	4.794	25.282
	D. res.		5.424	1.455	7.132	0.990	5.243	0.461	2.260	0.333
Sept 21	Tr. rate		26.500	29.220	22.970	19.490	25.620	33.490	32.120	33.060
	D. res.		0.340	0.252	0.500	0.550	0.452	0.193	0.240	0.208
Sept 22	Tr. rate		9.230	20.423	16.357	15.333	12.213	27.110	15.100	26.126
	D. res.		0.990	0.391	0.422	0.560	0.906	0.350	0.661	0.320
Sept 23	Tr. rate	Southern	3.500	16.840	5.432	16.766	6.757	30.387	8.324	25.099
	D. res.		5.250	0.666	6.824	0.480	1.945	0.634	1.794	0.590
Sept 24	Tr. rate		6.260	16.668	3.123	15.973	7.871	25.588	7.544	25.361
	D. res.		2.966	1.011	3.656	0.428	1.885	0.410	2.040	0.332
Sept 25	Tr. rate		4.654	16.606	3.491	15.634	5.829	26.596	5.720	25.493
	D. res.		5.950	0.740	3.280	1.064	1.950	0.380	2.230	0.330
Sept 26	Tr. rate		3.311	16.156	2.148	16.110	5.612	23.923	3.618	24.678
	D. res.		12.310	0.797	6.509	1.032	11.777	0.646	2.176	0.630

Table VI. Mean transpiration rates (μg/cm /s) and diffusive resistance (s/cm) in poplar cuttings at the end of the treatment period.

		Treatments	Heavy soil				Light soil			
			pH 3.0		pH 5.0		pH 3.0		pH 5.0	
Day	Parameter	Provenance	drought	control	drought	control	drought	control	drought	control
Nov 2	Tr. rate		6.041	5.408	9.347	6.886	4.962	4.351	7.311	6.005
	D. res.		4.243	3.439	4.011	3.358	4.354	3.740	5.199	3.267
Nov 3	Tr. rate		5.550	5.204	8.852	6.897	4.422	4.040	6.554	5.208
	D. res.		3.977	3.620	2.006	3.107	3.645	3.939	3.588	3.777
Nov 4	Tr. rate	Northern	6.036	4.130	5.002	5.378	3.172	3.471	3.761	4.841
	D. res.		3.569	4.818	3.457	3.943	5.823	5.634	5.290	3.864
Nov 5	Tr. rate		3.433	4.236	2.128	5.757	1.952	3.928	2.060	4.771
	D. res.		4.009	4.376	7.085	3.163	12.023	5.359	8.436	3.643
Nov 6	Tr. rate		1.749	4.138	1.729	5.657	1.359	3.584	1.273	5.085
	D. res.		9.203	5.221	8.685	3.664	13.590	5.485	11.503	3.616
Nov 7	Tr. rate		1.016	4.267	1.094	5.224	1.026	3.662	0.918	4.869
	D. res.		23.124	4.535	8.525	2.950	11.610	4.189	12.806	3.656
Nov 2	Tr. rate		11.746	5.661	8.052	8.239	7.576	5.198	9.235	4.778
	D. res.		1.836	3.367	2.465	2.877	2.993	3.679	1.980	4.158
Nov 3	Tr. rate		10.951	5.500	7.282	7.450	6.346	5.080	7.735	7.475
	D. res.		5.577	3.462	2.871	2.677	3.192	3.321	2.365	4.214
Nov 4	Tr. rate	Southern	5.611	4.340	8.851	7.243	4.065	4.947	5.135	4.416
	D. res.		1.054	4.394	4.584	2.863	4.553	3.731	4.034	3.994
Nov 5	Tr. rate		2.909	4.302	2.021	7.031	2.197	5.160	2.396	4.679
	D. res.		6.150	4.492	8.430	2.914	7.498	3.594	7.642	3.775
Nov 6	Tr. rate		1.854	4.198	1.095	7.076	1.612	4.958	1.603	4.617
	D. res.		11.784	4.394	12.749	2.900	9.755	3.872	10.493	3.991
Nov 7	Tr. rate		1.026	4.178	0.805	6.815	1.205	4.763	1.020	4.590
	D. res.		14.595	4.472	14.690	3.296	10.877	3.850	12.304	3.816