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Effects of wind induced soil moisture stress on the germination and early growth of Pinus banksiana Lamb. on three soil texture types

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The Effects of Wind Induced Soil Moisture Stress on the Germination and Early Growth of *Pinus banksiana* Lamb. on Three Soil Texture Types

By

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ABSTRACT

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Other Key Words: osmotic priming, permanent wilting point, soil characteristics, wind tunnel

A controlled environment wind tunnel was used to produce three wind speeds and hence three soil drying rates in order to study the effects of soil moisture stress on seeds and germinants of *Pinus banksiana* Lamb. planted in a sandy loam, loamy sand and sand. Osmotically primed and untreated seed were sown when the soil was saturated and germination was monitored daily. Germinants at five stages of ontogeny, the most advanced stage being the start of epicotyl growth, were placed into the wind tunnel with the soil saturated. When 50% of the germinants were dead and/or wilted, final length and dry weight of the shoots and roots were measured. All experiments were a split plot factorial design with wind speed as the main plots and the soil and seed or ontogeny stage treatments as the subplots.

No seed germinated in the wind tunnel for any of the soil type and wind speed treatment combinations. Therefore, seed were transfered from the soil surface to Petri-dishes in a germination cabinet where germination was monitored daily. Compared to controls (primed and unprimed seed taken from cold storage), germination of unprimed seed decreased with each increase in wind speed, the magnitude of the decrease varying with soil type. A similar response was not noted for the primed seed; osmotic priming appeared to negate the effects of the physical environment. The exact cause could not be determined from these studies. The hypothesis that the unprimed seed did not imbibe some critical, minimum amount of water before drying and that something inhibited germination when the seed was rehydrated is presented and discussed.

The fewer number of macropores and the more rapid drying rate of the loamy sand and sandy loam soil types was considered to be the cause of poorer establishment with increasing wind speed of the early ontogeny stages (stages up to the point the radicle has penetrated the soil surface and the seed is slightly elevated). The growth and survival of germinants once established was not affected by these factors. The data suggests that the drying rate of the soil and the inability of root growth to keep up with this drying was considered to be a major factor affecting growth and survival of the established germinants. Additionally, the transpiration rate of the germinants probably played a significant role in the survival time. The loamy sand and sandy loam soil types probably could not supply a sufficient quantity of water to the germinant to keep pace with the transpirational demand. The sandy soil was better for growth and survival than the finer soils probably because of the way water is held in the soil profile once the capillaries are broken. Germinants began to die at soil moisture potentials above the permanent wilting point (PWP) at the high wind speed. This supports the view that PWP is not a soil constant. The increase in some growth parameters with increasing wind speed supports the view that increasing wind speed is not always detrimental to germinant growth. Application of the results to field conditions is discussed.

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RFK

1. INTRODUCTION

Direct seeding is a major method for regenerating jack pine (*Pinus banksiana* Lamb.) in Ontario. Brown (1973) stated that direct seeding accounted for 20% of the total regeneration program for all tree species in the province at that time. In the intervening years, this has ranged from a high of 49% in 1981 to a low of 17% in 1985 (Anonymous, 1978,1982a, 1985a). Of the 20% of direct seeding mentioned by Brown (1973), 90% was performed with jack pine. This figure has probably not changed much in the last 14 years.

Adverse environmental conditions have long been recognized by researchers and foresters as being detrimental to jack pine seed germination and germinant survival (see the literature review), but it is the variability in seeding success (Alex Clarke, OMNR Kenora, personal communication) which is of the greatest concern and interest. At times, direct seeding has been too successful, resulting in greatly overstocked stands or in several trees per seedspot. At other times, very few seeds germinate and the direct seeding operation fails. In the former case, it is probable that environmental conditions at the time of germination or shortly thereafter (barring other factors) were favourable; whereas, in the latter case, they were not.

A silviculturalist may be able to improve direct seeding success and to reduce the variability of success by: 1) timing field activities to avoid environmental conditions that are unfavourable to seed germination and germinant survival, 2) avoiding direct seeding on sites that are considered unfavourable and electing to plant instead, 3) modifying the harvesting methods to ameliorate environmental conditions which are considered detrimental to direct seeding success, and 4) using site preparation methods that produce seedbeds that are most favourable for seed germination and for subsequent growth of jack pine seedlings.

To choose the best course of action, the silviculturalist needs to know the quantitative effects of the various environmental factors and factor combinations that are favourable or detrimental to seed germination and germinant survival. The better the relationships between weather, seedbed characteristics, germination and germinant survival are understood, the greater the control possible over direct seeding (Sutton, 1975).

Through the years, many researchers (see literature review) have cited moisture and temperature as the most influential environmental factors affecting germination of seed in the field. Even though both factors are considered to be influential, only temperature has been thoroughly investigated in terms of its

critical range and its effect on jack pine germination and germinant growth.

Quantitative information on the effects of moisture stress on tree species is needed (Scott,1966; Falusi et al., 1983). Glerum and Pierpoint (1968) state "It has long been appreciated that soil moisture deficits reduce plant growth. However, a quantitative knowledge is needed rather than a generalization". Quantitative information could be used to advance our understanding of the interaction of the plant and environment and could be used in growth models for trees (Perala, 1983).

Because soil moisture or any environmental variable is difficult to control and measure in the field, experiments need to be conducted under controlled conditions in the laboratory or greenhouse (Rees and Grace, 1980). Thomas and Wein (1985), Jeglum (1979) and Shepperd and Noble (1976) concur and have themselves conducted greenhouse moisture stress studies with jack pine, black spruce (*Picea mariana* (Mill) BSP) and lodgepole pine (*Pinus contorta* Dougl.), respectively. The use of controlled environment studies enables the researcher to learn about the magnitude and nature of plant response to a single variable (Rees and Grace, 1980) or combinations of variables. This knowledge can then be used as an aid in interpreting field experiments where environmental factors are not constant but react with each other in a multitude of ways.

The purpose of this research was to quantitatively study the effects of moisture stress on germination and initial development (to the stage of epicotyl development) of jack pine grown on three soil-texture types. Two studies were conducted: 1) a germination study and 2) an ontogeny study.

The objectives of the germination study were to determine the effects of various soil moisture potentials on seed germination and to observe the effects of continued drying on the germinants. The objectives of the ontogeny study were to observe the effects of moisture stress on the morphological attributes of germinants at various stages of ontogeny and to determine the soil moisture potentials at which these germinants begin to die.

The experiments were conducted as a pot study in a controlled environment wind tunnel constructed for this research and located in a greenhouse. Within the wind tunnel, air temperature and humidity, both of which affect soil moisture evaporation, transpiration, seed germination and germinant growth, were held constant. Unfortunately, ultra violet radiation could not be controlled; it varied with conditions encountered in the greenhouse at the time of the experiments. Moisture stress was induced by withholding water and subjecting the soil to different drying rates by the use of three wind speeds.

In these experiments, unlike many other moisture stress experiments, moisture tension of the growing medium was not held constant but continually decreased from saturation to more negative potentials. This more closely simulates conditions experienced by seeds and seedlings germinating and growing in the field. Studies have been conducted using constant water potential levels; however, it is difficult to extrapolate the results of these studies to the more natural situation where water potential continuously fluctuates (Kaufmann, 1968). Conditions of constant water potentials rarely occur in the

field since periods of precipitation are followed by subsequent drying (Thomas and Wein, 1985). This produces repeated fluctuations in soil moisture availability.

When this thesis was started in the fall of 1983, no quantitative study observing the effects of moisture stress on jack pine germination had been conducted. Thomas and Wein (1985) cite a doctoral thesis in which the effects of constant moisture stress and intermittent watering of a soil medium on germination was investigated. These experiments were the first of their kind with jack pine. My research still differs from these studies because in it I impose increasing soil moisture stress on the seeds and germinants and do so with wind.

2. LITERATURE REVIEW

2.1 INTRODUCTION

The relationship between a seed and seedling and its environment is complex. Because of this complexity moisture stress research encompasses a diversity of subject areas (i.e. soil physics, plant physiology, climatology) of which a reader must have some knowledge if they are to understand aspects of the methods, results and discussion in this paper. In an effort to present much of the pertinent material, this is a lengthy literature review that covers a wide range of topics. This could not be avoided given the diversity of topics reviewed and the volume of material available. Where the topics are broad only material directly related to this thesis are presented and references for further reading are given.

It is recommended that all readers review sections 2.2 to 2.5 in order to obtain background information about the various factors affecting seed germination and seedling growth and to review the current level of understanding of the effects of temperature and moisture on jack pine. Section 2.5 is a review of moisture stress research conducted with other tree species. From this section the reader will gain an appreciation of the type of research which is lacking for jack pine. The balance of the sections (2.6-2.13) review various topics applicable to this research and may be used as review or as reference.

2.2 FACTORS AFFECTING FOREST TREE SEED GERMINATION AND SEEDLING SURVIVAL

Many factors have been cited as contributing to poor seed germination and seedling survival in the field. These factors are (in random order) 1) lack of site preparation, 2) destruction of seed by rodents and birds, 3) lack of suitable seedbed, 4) temperature, 5) moisture, 6) frost heaving, 7) winter injury, 8) insects, 9) disease, 10) damping off, 11) light, 12) movement of seed by wind and water, 13) high winds, 14) poor distribution of seed, 15) poor or excessive aeration and 16) biocides .

These factors have been cited by some or all of the following authors: Eyre and LeBarron, 1944; LeBarron, 1944; Fraser and Farrar, 1953b; Roe, 1963; Cayford, 1963, 1966; Scott, 1964; Matte et al., 1964; Benzie, 1965, 1977; Marquis, 1967; Kaufmann and Ross, 1970; Scott, 1970; Kozlowski, 1971; Buckner, 1972; Sims, 1970, 1975a, 1975b; Arnott, 1974; Riley, 1975; Shepperd and Noble, 1976; Bewley and Black, 1978; Kramer and Kozlowski, 1979; Wagenvoort, 1981; Berkat and Briske, 1982.

Of the 16 factors above, temperature, moisture and rodents are considered to be the three most influential factors on seed germination and stand regeneration. Fraser and Farrar (1955) state that "The

chief external factors influencing germination [of jack pine] are moisture and temperature". Preliminary observations indicated that lethal surface temperatures and drought were factors contributing to jack pine regeneration failures on dry sites (Sims, 1975a). Larson and Schubert (1969) note that a major obstacle to ponderosa pine (*Pinus ponderosa* Laws.) regeneration is drought and that entire crops of seedlings have been lost while the roots have been in the upper foot of soil. Sims (1970), in his experiment with the Middle Buster Plow in Manitoba, found that "Heat combined with drought was a major cause of mortality on the dry and moderately fresh sites". Between the stages of germination and when juvenile needles are formed, heavy losses may be incurred as a result of dry weather, particularily if it is accompanied by high temperatures (Shirley, 1937). In the Lakes States, Shirley (1937) felt that high soil surface temperatures were more important than drought as a cause of seedling mortality.

The effects of rodents and birds are also cited by many authors. Roe (1963) states that "Probably the most important reason for poor initial stocking of seeds was the loss of seed to rodents and perhaps birds". Sims (1975a) found that mortality caused by animals was severe at times but highly variable ranging anywhere from 2 to 35%. Buckner (1972) found that depredations by small mammals of the seed and seedlings of trees in the coniferous-praire zone is among the most important production problems. In certain instances, the other factors may also be very influential; but, generally speaking, temperature, moisture and rodents are the most influential.

A distinction between the effects of drought and temperature problems and rodent problems can be made. Predation by rodents and birds affects the total number of seed that may germinate and survive. The effects of heat and moisture determine the percentage of the total seed available that actually germinate and survive. The number of seed available for germination can be controlled easily by artificial means but the number of seed which actually germinate requires a greater understanding of the interaction of the seed and its environment and is more difficult to control on a large scale.

Of the three influential factors, rodents and birds are the easiest to control. Trapping, baiting and seed coating may be used to reduce the effects of rodents on the seed supply; however, little can be done to ameliorate economically the effects of temperature and moisture. Consequently, a greater understanding of how these factors influence germination is desired.

2.3 TEMPERATURE AND JACK PINE

For jack pine, of the three most influential environmental factors affecting germination and growth, temperature is the most researched. The definitive work on the critical temperature range for jack pine germination was performed by Fraser (1970). The objective of Fraser's (1970) study was to determine the cardinal temperatures for the germination of two provenances of white, red and jack pine. He defined cardinal temperatures for germination as "... the temperatures below which seeds do not germinate, the temperatures above which seeds do not germinate and the temperatures or temperature range at, or within

which maximum germination occurs in a stipulated period of time".

Fraser (1970) found that, for jack pine, the upper critical temperature for germination is 40.5°C, the lower critical temperature is 10°C and the optimum critical temperature range is 15.5°C to 35.0°C. At the upper and lower critical temperatures, germination responses were 20% or less or "... too slow and irregular to warrant further consideration" (Fraser, 1970). The study was conducted in petri-dishes with adequate moisture.

Fraser's (1970) results are supported by observations of others. Eyre and LeBarron (1944) noted that "Under favourable moisture conditions, jack pine seed will germinate rapidly whenever the 10 day mean maximum air temperature is 65°F [18°C] or higher". Eighteen degrees celcius corresponds closely to Fraser's (1970) lower critical value of 15.5°C. Sims (1970) observed similiar results.

Fraser and Farrar (1953a) noted that where germination was poorest, soil surface temperatures of over 43°C were recorded. Sims (1975a) noted that there were sufficient data in the literature to indicate that 49°C was the lethal upper temperature limit for jack pine in the first year. These results also relate well to Fraser's (1970) findings.

The above authors have quantitatively defined the temperature range for jack pine seed germination both under laboratory and field conditions. Moisture requirements for jack pine seed germination have not been quantified to the same degree.

2.4 MOISTURE AND JACK PINE

2.4.1 GERMINATION

As noted in the introduction, at the time this research was started in 1983 no quantitative study investigating the effects of soil moisture on the germination of jack pine was found. Since then, Thomas and Wein (1985) observed that jack pine germination was not significantly reduced ($p \leq 0.001$) above -12 bars of osmotic potential. Additionally, using a soil medium and watering frequencies of 2, 8 and 12 days, they found that percent germination was reduced with more widely spaced watering frequencies.

Several qualitative studies and observations were found in the literature. Ellis (1911) made the general comment that "Compared with its associates it [jack pine] will withstand considerable drought and frost and it is altogether peculiarly adapted to thriving under xerophytic conditions". Li (1940) stated that "... no one has ever determined exactly how much water seedbeds should have to effect the best germination". Li investigated the effects of imposed moisture stress on jack pine and red pine, by germinating seeds in boxes of soil (38 x 38 x 15 cm) watered at varying intervals. He found that the best germination of jack pine seed was in boxes watered every 5 to 6 days with 2 quarts of water. Seedlings in these two treatments were 25% heavier than seedlings in any of the other treatments. Sims (1970) found that "Total germination and mortality increase and decrease, respectively, from dry to fresh habitats".

The purpose of an experiment by Fraser and Farrar (1953a) was "... to show how the germination of seed [jack pine] is affected by manipulating certain factors of the environment associated with moisture and temperature". They manipulated the environment by shading, watering and planting the seed at different depths and in different mediums. Two gross watering regimes were used: 1) natural precipitation only and 2) the addition of 0.125 inches (3 mm) of water daily if the previous days rain did not exceed 0.25 inches (6 mm).

Conditions favouring a high moisture content in the seed resulted in good germination (Fraser and Farrar, 1953a). These conditions were 1) use of a fine textured medium, 2) addition of water, 3) shading and 4) placing seed below the medium surface. They also noted that the results depended on one another. One could not mention the effects of moisture without stating the soil type and light level. Matte et al (1964) made similar observations. "A seedbed of fine sand mineral soil, sowing depth of about 1/4 inch [6 mm], and partial shading of the seedbed permit optimal water relations for germination and early growth of jack pine..." (Hacker et al., 1983).

The problem with all but Thomas and Wein's (1985) experiments is that they do not give a quantitative estimate of germination at specific levels of soil moisture potential or over a range of soil moisture potentials. Granted, they do relate the effects of moisture on germination; however, this serves only to support the point that moisture is a critical factor of jack pine seed germination. The results do not quantitatively relate soil moisture content to the percentage of germinated seed.

2.4.2 POST-GERMINATIVE GROWTH

Few references about the effects of mositure stress on post-germinative growth of jack pine were found. An indirect reference was made by Eyre and LeBarron (1944). They state:

> Although jack pine seedlings can grow on sterile, droughty soils, they are very responsive to their environment. Unlike the seedlings of most other conifers in the region, they do not during the first growing season form definite terminal buds and cease height growth in midsummer; instead, they start and stop growth according to temperature and moisture conditions, sometimes continuing height growth late into the fall.

McClain and Armson (1975) investigated the effects of moisture-fertility interactions on jack pine, black spruce and white spruce for possible management application in nurseries. They found it very difficult to regulate and monitor soil matric suction; therefore, they resorted to a schedule of water application. They applied water at 3, 5, and 9 day intervals and broadly classed the soil moisture regimes as very moist, moist and moderately dry. Mortality of jack pine germinants was highest for the moderately dry moisture regime. Dry weight increased with increasing soil moisture content. The rate and duration of height growth was greater in the very moist than in the moist and moderately dry moisture regimes. The dry weight and height results were consistent for all fertility levels.

Ellis (1911) noted that the optimum soil water content for jack pine development varies from 10 to 20 percent.

It is evident from the few citations above that quantitative information on the effects of moisture stress on jack pine germinants is lacking. For jack pine, it appears that the major thrust of most moisture stress research has been on the effects of moisture stress on germination rather than on the germinant; however, considerable information on moisture stress effects on germinants is available for other species.

2.5 MOISTURE AND OTHER FOREST TREE SPECIES

2.5.1 GERMINATION

Several studies have considered the effects of moisture stress on forest tree seed germination. Satoo (1965) studied the germination of *Pinus densiflora* Sieb.&Zucc (Japanese red pine), *Pinus thunbergii* Parl (Japanese black pine) and *Chamaecyparis obtusa* (Hinoki cypress) and found that the highest germination percent occurred at approximately 50-60% soil moisture content (dry weight basis) (64.3% was field capacity). Bonner and Farmer (1966) germinated sweetgum seed (*Liquidambar styraciflua* L.) at different temperatures and osmotic potentials. They found "... that at favorable temperatures, properly stratified seed will attain maximum germination under 5 atmospheres and acceptable germination (80 percent or more) at ten atmospheres".

Larson and Schubert (1969) noted that "Osmotically induced water stress strongly influenced both germination percent and germination value of ponderosa pine seeds...". They found that potentials less than -7 bars drastically reduced both germination percent and germination value. The germination percent of longleaf (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Engelm.) decreased significantly for every increment of soil moisture potential (an osmotic solution of d-mannitol) beyond -2.5 atms (Barnett, 1969). The greatest decrease occurred at eight atmospheres. Moisture stress not only affected final germination percent but delayed the start of germination and reduced the rate at which it occurred (Barnett, 1969).

These studies indicate that it is possible to quantify the effects of moisture stress on forest tree seed germination. Forest research on this topic, however, pales in the light of the research which has been conducted with agricultural species. References in the literature are numerous. Wagenvoort (1981) notes that for agriculture and horticulture, knowledge of the relationship between germination and moisture tension is essential if optimum germination and seedling growth is to be attained. This is also very much the case in forestry especially with the current expenditures for forest regeneration under Forest Management Agreements (FMA's) in Ontario.

2.5.2 POST-GERMINATIVE GROWTH

The effects of moisture stress on post-germinative growth of tree species have also been investigated. The effects of moisture stress on germinants in which the radicle has only started to emerge, have been investigated by Larson and Smith (1969) using ponderosa pine and white pine (*Pinus strobus* L.) and by Larson and Devault (1974) using ponderosa pine. Seed were allowed to germinate to various levels of radicle elongation and air dryed for set periods before being re-watered. In both studies, the results indicate that the seeds will recover from the stress after re-watering provided that the radicle has not elongated more than 2-3 mm; however, seedling vigour is reduced during the first weeks. Djavanshir and Reid (1975) found that radicle elongation of ponderosa pine was severely reduced at osmotic potentials of -4 bars and less.

Root penetration, root dry weight and cotyledon length of ponderosa pine germinants, grown in test tubes filled with vermiculite saturated with an osmotic solution, decreased significantly with decreasing potential of the solution (Larson and Schubert, 1969). "Epicotyl growth decreased with a decrease in osmotic potential from 0 to -3 bars... Below -3 bars, cotyledon emergence from the seedcoat and epicotyol growth progressively diminished to zero at -15 bars" (Larson and Schubert, 1969).

Kaufmann (1968) used drying cycles of different length and therefore of different severity as his water potential treatments when studying the root growth of loblolly pine (*Pinus taeda* L.) and white pine seedlings. Root growth was less uniform than needle growth during the drying cycles. Kaufmann (1968) attributed this to a tendency of the roots to mature toward the tip and become dormant. This occurred even after a single period of drought even when watering was resumed on a daily basis. Falusi et al. (1983) observed that water stress significantly reduced root length of Alleppo pine (*Pinus halepensis* Mill.) between -2 to -6 bars of osmotic potential depending on provenance.

Zahner (1968) presents a discussion of the effects of moisture stress on the shoot growth of seedlings of woody plants. He notes that shoot growth is affected by relatively low soil moisture potentials. Shoot dry weight of one year old Scots pine (*Pinus sylvestris* L.) seedlings was affected by soil moisture tension of -0.5 bars (Sands and Rutter, 1959; cited in Zahner, 1968). Jarvis and Jarvis (1963, cited in Zahner, 1968) found that shoot dry weight of Scots pine and Norway spruce (*Picea abies* (L.) Karsten) was reduced 33% at a soil moisture tension of -1.7 bars.

The effects of drought on yellow-poplar seedlings (*Liriodendron tulipifera* L.) was investigated by Loftus (1975). He found that seedling height growth was reduced slightly by increasing moisture tension imposed by drying periods of 7,14 and 21 days before re-watering to field capacity. Diameter and shoot dry weight were reduced at -2.4 bars and shoot growth and root development were inhibited at -4.0 bars. Height growth of loblolly and slash pine was inhibited by soil moisture tensions not greater than -2.0 bars and stopped completely as tension increased to -3.5 bars (Stransky and Wilson, 1964).

Again, as with seed germination, quantification of the effects of moisture stress on germinant

growth is possible. Unfortunately, such information is lacking for jack pine. As above, this information can be used to further our understanding of the relationship of the plant to its environment in order to attain optimum growth.

2.6 SEED DORMANCY

The seeds of many woody plants exhibit dormancy, that is, they fail to germinate when placed under favourable environmental conditions (Kramer and Kozlowski, 1979). "Dormancy is normally the result of the interaction of imposed environmental conditions and the hereditary properties of the plant" (Schopmeyer, 1974). There are two major categories of dormancy, physiological and physical. In the former case, physiological changes must occur within the embryo or within the the cotyledons, seedcoat or endosperm of the seed before the seed will germinate. Included in this category are species which have chemical inhibitors within the seed which prevent germination.

Physical dormancy is the result of a morphological characteristic of the seed. Examples of physical dormancy are seed coat impermeability to water or oxygen or seed coats which mechanically restrict the enlargement of the embryo. Under natural conditions seed dormancy is not overcome until the seed receives the proper environmental stimulus. For more detailed information about seed dormancy see the reviews by Kramer and Kozlowski (1979), Harper (1977) and Schopmeyer (1974).

It is generally accepted that jack pine does not have dormant seed. Rudolph (1958) and Fowells (1965) note that jack pine occassionally exhibits dormancy but usually germinates within 15 to 60 days under favourable environmental conditions. Some seed, however, requires more than 100 days to germinate (Rudolph and Yeatman, 1982). Delayed germination has been observed in several direct seeding trials in Ontario.

Kokocinski (1965) observed that after direct seeding a repeatedly burned cutover, approximately 92% of the jack pine regeneration became established over a three year interval. The site was repeatedly burned over a short time interval before seding thus natural seeding could not occur. Therefore, Kokocinski felt that the large numbers of seedlings over the three year time interval was the result of delayed or prolonged germination. Similar observations were made by Scott (1970), Riley (1980), Hacker et al. (1983), Smith (1984) and Thomas and Wein (1985b). Kokocinski states that "...by remaining dormant and retaining its viability, a portion of the sown seed could avoid the post-emergence hazards of a poor growing season. It might then be available for [prompt] germination when conditions are more favourable". A poor growing season was one in which precipitation was limited.

Although jack pine does not exhibit physiological or physical dormancy it does exhibit delayed germination. This delayed germination could be considered dormancy. The cause of the the delay is not known but may be moisture related.

2.7 EFFECTS OF SITE

Many authors have observed that site has a definite effect on the total germination and mortality of individual seedlings. Cayford (1963) observed that site had a profound effect on jack pine mortality. On a dry site, over 50% of the seedlings died as compared to only 2% on a moderately fresh site. Scott (1966) reviews a number of direct seeding projects in Ontario and comments on their success with respect to site. Sims (1970) in his experiment with the Middle Buster Plow in Manitoba, found that on the dry sites germination was consistently low and mortality was very high when compared to the moderately fresh and fresh site.

In Cayford's and Sims' experiments above, a dry site was characterized by coarse sands and water tables well below the rooting zone. They found that on fine sand, germination was high, regardless of the level of the other environmental factors being controlled; but, on coarse sand germination was poor due to dryer conditions. In Fraser and Farrar's (1953a) study, even with irrigation and full light, germination of surface sown seed was poor on coarse sand.

Field observations indicate that site and particularly the soil texture of the site has an effect on the germination of seed and the survival of germinants. This occurs because soil texture affects soil moisture retention, the movement of water in the soil (the hydraulic conductivity and flux of soil moisture) and seed soil contact (Brady, 1974; Mayer and Poljakoff-Mayber, 1975; Hillel, 1982). Therefore soil texture must be a factor considered in any study investigating the effects of moisture stress on seed germination and germinant growth.

2.8 SOIL PHYSICAL PROPERTIES IN RELATION TO GERMINATION AND POST-GERMINATIVE GROWTH

Reductions in germinative energy, germination percent and post germinative growth as a result of moisture stress have been attributed to several factors. These factors are: 1) soil moisture content and hydraulic conductivity, 2) the soil solution osmotic protential, 3) the seed-soil (root-soil) contact area (Hadas, 1970) and 4) soil microclimate and microtopography (Harper et al., 1965). These four factors are discussed separately below.

2.8.1 SOIL MOISTURE CONTENT AND HYDRAULIC CONDUCTIVITY

2.8.1.1 THEORY

The topic of soil physics is too voluminous and complex to present a thorough review here. Material relevant to this research are briefly presented below. See Brady (1974), Pritchett (1979) and Hillel (1982) for more detailed information.

The amount of water retained in the soil at any given matric potential depends primarily upon soil texture. Matric potential (suction) is due to the physical affinity of water to the soil-particle surfaces and capillary pores (Hillel, 1982). Soil characteristics which affect water retention are the capillary effect, pore size distribution and the specific surface of the soil medium (Hillel, 1982). Generally, the higher the clay content of the soil (i.e. the finer the texture), the more water retained by the soil at a given soil matric potential (Brady, 1974; Hillel, 1982). The water is retained in the wedges between adjacent particles and as a thin film over the particles. In a finer soil there are more wedges and more finer particles thus more surfaces for attracting moisture. In a sandy soil, the pores are relatively large and fewer fine particles are present for holding moisture. Therefore, once these large pores empty there is a minimal amount of water available at a given suction. There are fewer wedges and the particles are larger in a coarse textured soil; hence, there is less water held at a given suction.

The flow of water in soil is in response to differences in the matric potential in different zones of the soil matrix. Hydraulic conductivity or the rate of water movement in a soil is a function of the soil properties and the properties of the fluid (Hillel, 1982). The soil characterisitics which affect hydraulic conductivity are total porosity (pore volume of the soil), the distribution of the pore sizes and tortuosity (the indirectness of the water path through the pores). The fluid characteristics which affect hydraulic conductivity are fluid density and viscosity. Hydraulic conductivity is different when soils are saturated as opposed to when they are unsaturated.

When saturated, coarse textured soils have a higher hydraulic conductivity than do fine textured soils (Brady, 1974; Hillel, 1982). Because coarse textured soils have a preponderance of large pores, water moves rapidly through these pores over a short period of time. However, when the soil is unsaturated there is insufficient water to continuously fill the large pores, capillary moisture films are discontinuous and water movement is reduced. The decrease in hydraulic conductivity as the soil becomes unsaturated may be of several orders of magnitude (sometimes down to 1/1,000,000 of its volume at saturation) as suction increases from 0 to 1 bar (Hillel, 1982). It is interesting to note that when a coarse textured soil is unsaturated, "...water sometimes remains almost entirely in capillary wedges at the contact points of the particles, thus forming separate and discontinuous pockets of water" (Hillel, 1982). When unsaturated, fine textured soils, with their preponderance of small pores, still retain many continuous capillary moisture films. Thus, fine textured soils can retain and conduct water at lower moisture potentials and therefore can conduct more water than coarse textured soils. This explains why coarse textured soils cannot supply moisture to the germinating seed for a long period of time at lower soil moisture potentials and why texture is a critical site factor.

Compaction of the soil decreases the total porosity of the soil, especially the volume of the large interaggregate macropores (Hillel, 1982). This results in a reduction in the total amount of water the soil can hold when saturated and affects the water loss associated with the initial application of low suction."On the other hand, the volume of intermediate-size pores is likely to be somewhat greater in a

compact soil (as some of the originally large pores have been squeezed into intermediate size pores by compaction), while the intraaggregate micropores remain unaffected" (Hillel, 1982). As a result of compaction, an originally coarse soil may now be able to hold more water at a given suction because the large pores have been squeezed into smaller ones. Compaction also affects the hydraulic conductivity of the soil. If the soil was fine, squeezing the pores reduces the size of the channels for moving water and the hyrdraulic conductivity of the soil may be reduced.

It has been shown that sand mulches over a finer textured soil effectively reduce evaporation from the soil profile, thus conserving soil water (Modaihsh et al., 1985). This was attributed to the inability of water to move up through the sand mulch (a function of soil texture and hydraulic conductivity) and closer to the source of evaporative energy. This may be advantageous for deep rooting species under arid conditions since moisture will be protected from evaporative loss (Koller, 1972).

Water vapour movement in the soil does occur. Brady (1974) notes that soil water vapour may be a major contributor of water to plant roots, whereas Hillel (1982) feels that the effects of water vapour movement are negligible, given no large temperature variations. Movement is dependent upon the vapour pressure difference between parts of the soil and on soil temperature differences (Brady, 1974; Hillel, 1982). Water vapour will move from warm to cold soil materials in response to vapour pressure differences. Additionally, water vapour will move as a result of soil water osmotic potential. This will be discussed in more detail below.

Evaporation from soil, without a water table close to the surface, occurs in three distinct stages (Hillel, 1982). Assuming that atmospheric evaporation is constant, they are:

1.) The constant rate stage. This stage occurs early in the process when the soil is wet and able to supply water to the soil surface at a rate sufficient to meet the evaporative demand of the soil. The evaporative demand is controlled by external environmental conditions (i.e., radiation, wind air humidity, etc.) and may be influenced by surface conditions. In dry climates this stage is usually brief, lasting from several hours to a few days.

2.) The falling rate stage. This is an intermediate stage during which evaporation falls gradually below the potential rate. During this stage, the evaporation is limited by the rate at which the gradually drying soil can deliver moisture to the zone of evaporation; hence, it is controlled by the soil characteristics.

3). The residual slow-rate stage. This stage eventually occurs and may last for days, weeks or months. This stage occurs when the surface-zone of the soil is so dry that further liquid water conduction through it effectively ceases. The only means of water movement is by the slow process of vapour diffusion and is thus affected by the vapour diffusivity of the surface soil.

The first stage of drying will last longer for fine textured soils than for coarse textured soils, since finer textured soils still have some unbroken capillary moisture films and can retain higher wetness values and conductivities as suction values become higher (Hillel, 1982).

During the first stage, moisture gradients in the soil profile become steeper as the soil surface becomes dryer. The continuation of evaporation results in the movement of a drying front into the soil profile as more water is lost from the soil profile as a whole. Hillel and van Bavel (1976) note that differences in soil hydraulic properties can influence cumulative evaporation from the soil. In a study with pure soil texture types (i.e. sand, silt, clay) they found the coarse-textured soils (sands) had the least evaporation and fine textured soils (clay) the most.

It is evident that the soil physical characteristics have an effect on moisture content, retention, movement and evaporation within the soil matrix. The physical characteristics of a soil would therefore also have an effect on germination and growth due to the dependance of these activities on soil moisture. Evidence of this is presented below.

2.8.1.2 EFFECTS ON GERMINATION

Soil matric potential and hydraulic conductivity affect the germination rate and total germination. Collis-George and Sands (1959) state that "All other physical factors being constant, the water uptake by seeds would appear to be controlled by both suction and the hydraulic conductivity of the soil". This point is supported by Hadas (1970) and Syvertsen (1985). Each species has its own water requirements in terms of suction and conductivity. This in combination with the suction and conductivity characteristics of the soil determines and distinguishes the germination character for that species in that soil system (Collis-George and Sands, 1962).

Movement of water to the seed is dependent on the hydraulic conductivity of the soil. Water potential of a dry seed can be as low as -1000 atmospheres and thus there is a great moisture potential gradient between the seed and the soil (Manohar and Heydecker, 1964). As the seed imbibes water, its water potential rises (i.e. becomes less negative) and the potential of the soil adjacent to the seed falls (i.e. becomes more negative). Since the seed cannot move towards the water, successful germination depends on the movement of sufficient water to the seed surface.

What makes this point even more critical is that "The distance over which water flows to the seed often does not exceed 10 mm, irrespective of the soil water content..." (Bewley and Black, 1978). Unless a sufficient amount of water can move through the soil to this zone around the seed in response to losses due to evaporation and seed use, the germination process will be affected.

The seed can partially offset the negative effects of rising water potential with imbibition. As the seed imbibes water, the high molecular weight storage material becomes depolymerized and osmotically active. This results in a decrease in what would otherwise be an increase in water potential (Koller, 1972). Additionally, as the seed imbibes water it swells thus increasing the surface area and the area of soil around the seed from which it can draw moisture (Koller, 1972). Seed-soil contact will be discussed in more detail in a subsequent section.

The complex influence of soil characteristics on soil water and germination, as mentioned above, is apparent in Jeglum's (1979) greenhouse study of different seedbeds and watering intervals on black spruce germination and initial growth. Jeglum found that the highest germination was associated with a sand substrate and not a clay substrate, given the watering frequencies used. This is opposite to what is expected given the previous discussion about moisture retention and hydraulic conductivity. Shirley (1937) notes that the most important characteristic of the soil is that it be moist near the surface during the germination period. Loams, silts and clay loams are more likely to be moist than sandy soils (Shirley, 1937). Thus Jeglum's (1979) better germination and initial growth on sand might appear to be a contradiction.

The inferiority of the clay substrate when compared to the sand substrate in Jeglum's study could be due to the poorer water supplying capacity of the clay. Jeglum (1979) felt that although the clay soil retains moisture more readily than other soils, it may not supply moisture as readily to seeds and germinants. The clay may have also produced a condition of poor aeration and drainage and the compact nature of clay may not have allowed radicle penetration. Jeglum also observed reduced crown and root length on clay in comparison with the sandy soil and other soil types.

Jeglum's results are supported by an uncited study mentioned by Scott (1966). The failure of a direct seedling project was attributed to sowing on clay loam. These results, however, may have been masked by other factors such as flooding and mid-summer sowing (Scott, 1966).

It is apparent from the above discussion that soil texture does affect seed germination. Because the seed cannot move towards the moisture it is dependent mainly upon water movement toward the seed. The movement of water and the availability of water in the soil is affected by the soil texture and its effects on soil moisture potential and hydraulic conductivity.

2.8.1.3 EFFECTS ON POST-GERMINATIVE GROWTH

Because soil moisture potential and hydraulic conductivity can also impose limitations on water availability to roots, they are not only important to seeds for germination but to plants for survival (Syvertsen, 1985). The same physical principles apply except in the context of roots rather than seeds.

The amount and rate of water uptake by a plant is dependent on a variety of factors. Hillel (1982) notes that

> The amount and rate of water uptake depend on the ability of the roots to absorb water from the soil with which they are in contact, as well as on the ability of the soil to supply and transmit water toward the roots at a rate sufficient to meet transpiration requirements. These, in turn, depend on *properties of the plant* (rooting density, rooting depth, and rate of root extension, as well as the physiological ability of the plant to continue drawing water from the soil at the rate needed to avoid wilting while maintaining its vital functions even while its own water potential decreases); *properties of the soil* (hydraulic conductivity-diffusivity-matric suction-wetness relationships); and also to a considerable extent the *meteorological conditions* (which dictate the

rate at which the plant is required to transpire and hence the rate at which it must extract water from the soil in order to maintain its own hydration).

Rawinski et al. (1980) found that four year old container planted seedlings of jack pine grew better (height growth) on the coarser soil texture types. They regressed height growth against the clay content of the soil obtaining a correlation coefficient of -0.80. As clay content of the soil increases, height growth of jack pine decreases. Rawinski et al. (1980) admit that other textural characteristics which are not accounted for in the regression may have some effect on seedling growth (i.e. surface runoff, soil compaction, frost heaving and aeration). Not only does inadequate soil moisture affect the water supply to the roots, it possibly reduces root conductivity directly by causing increased suberization of the roots (Syvertsen, 1985).

Dosskey and Ballard (1980) investigated the resistance of water uptake by Douglas-fir seedlings at various soil water potentials and with different soil textures (loamy sand, silt loam and silty clay). They found that there were large differences in the average resistance and uptake rate of plants between unsaturated soils of different texture and attributed these differences to the soil texture. The resistance offered by soils of different textures may affect the ability of plants to meet the transpirational demand of the atmosphere and result in stomatal closure in response to negative leaf water potential. Loamy sand offered the most resistance and silty clay the least resistance to water uptake to roots. Blizzard and Boyer (1980) feel that as soil moisture potential decreases (becomes a larger negative value) it is unclear whether the resistance to water movement is greater in the soil or in the plant. In their study with soybean, plant resistance to water movement increased as soil resistance to water movement increased, the former being higher than the latter for the range of soil moisture potentials they studied.

Faiz and Weatherley (1977, 1978) investigated the changes in soil moisture potentials between the root systems of plants and the soil at the time the plants were subjected to high rates of transpiration. They concluced that the resistance of water movement to the root occurred at the soil-root interface.

Faiz and Weatherley (1982) also tested the hypothesis that the resistance at the soil-root interface could increase as a result of the contraction of stressed roots with the formation of vapour gaps between soil and roots. The study revealed that the roots did indeed contract and that this resulted in an increase in the hydraulic resistance of flow into the roots. A change in relative diameter of the roots of 19.9% resulted in a fall in water potential of 9.9 bars. They note, however, that the contraction of the root could not initiate a rise in the resistance of the root-soil interface since an initial increase in resistance is needed to result in a decrease in the root water potential and hence cause contraction.

Not only do soil characteristics affect the moisture relations of the soil and the plant, they also affect seedling root growth directly. Soil texture, more specifically the number of macro and micropores present in a soil, affects the establishment and root growth of seedlings. Root penetration of the soil and root elongation is reduced as the number of continuous macropores (diameter $\geq$ 60 μm) decreases in the soil (Russell 1977; Kramer, 1983). This occurs mainly because roots are usually in excess of 60 μm in

diameter and have a hard time penetrating pores that are smaller in diameter (Kramer, 1983). If the roots have to exert any force to expand the pore such that they can enter, then root elongation is reduced. Wiersum (1957) found that roots could not reduce their diameter to enter a small pore space, in fact, when their elongation was restricted by external pressure, their diameter usually increased. An excellent discussion of the effects of pore structure on the growth of roots can be found in Russell (1977). It must be noted that the above trends were observed on roots of mature plants, not on the radicles of seeds.

Pomeroy (1949) found that both seedling establishment and rooting depth were affected by the soil texture. The ability of the radicle of germinating loblolly pine seed and the roots of established seedlings to penetrate the soil was affected by soil texture. Root penetration of a clay loam soil was signficantly less than that in either a very fine sandy loam or a sand.

From the information presented in sections 2.8.1.2 and 2.8.1.3, both germination and seedling establishment and growth are affected by soil texture. Therefore, soil texture must be a factor considered in any research investigating the effects of moisture stress on a species.

2.8.2. SOIL SOLUTION OSMOTIC POTENTIAL

Osmotic potential results from the presence of solutes in the soil water (Brady, 1974; Hillel, 1982). These solutes lower the potential energy of the soil, specifically, the vapour pressure of the water (Hillel, 1982); however, this has little effect on the liquid movement of water in soils. "In non-saline soils, matrix forces normally play the most important part in lowering the water potential..." (Manohar and Heydecker, 1964; Koller, 1972).

Liquid and vapour movement of water can occur independently of each other along their own potential gradients (Kramer, 1983). In the soil profile, water vapour moves from a region of high vapour pressure to an area of low vapour pressure in response to a diffusion gradient.

The main effect of osmotic potential is on the uptake of water by plant roots and seeds and on processes involving vapour diffusion in the soil (Brady, 1974; Hillel, 1982; Kramer, 1983). Osmotic potential affects the water uptake of plant roots and of seeds because these processes are contolled by semi-permeable membranes.

2.8.3 SEED-SOIL CONTACT AREA

In the literature, there is evidence to indicate that seed soil contact area plays a role in the absorption of water and the germination rate of seeds. Hadas (1970) states that "Low hydraulic conductivity and small seed-soil contact area may reduce the water flow toward the seed". As soil dries, the contact area between the soil particles and the seed surface become a critical factor (Manohar and Heydecker, 1964; Mayer and Poljakoff-Mayber, 1975). Good seed soil contact was considered important by Harper and Benton (1966)

in order that the seeds have a net gain in absorbed water. They found when the seed is on the soil surface, the seed not only absorbs water from the soil, but also loses water to the atmosphere.

Germination is affected not only by seed-soil contact but also by the properties of each seed, how it lies, the shape of the seed and the evaporating power of the atmosphere at the time of germination (Mayer and Polojakoff-Mayber, 1975; Harper, 1977). Dessication of small seed has been found to be less then for large seed because the small seed has a large contact/surface ratio (Harper and Benton, 1966). Seed soil contact was found to improve if the size of the seed was less than the particle size of the soil and if the seed had a smooth surface (Harper and Benton, 1966; Bewley and Black, 1985).

Koller (1972) notes that it is not the contact between the soil particles and the seed that is critical but that between the seed and the pores which hold the water. The size of the seed relative to the soil particles affects the distribution of pores in contact with the seed. Soil pores with a large effective diameter are favoured. "These are the pores from which least energy is required to withdraw water and they will be the first to drain as soil moisture is depleted. Therefore, relatively small reductions in soil-moisture content are liable to result in disproportionately large reductions in contact area between the seed and soil water" (Koller, 1972).

Conifer seeds absorb water as long as any part of the pericarp is in contact with water (Goo, 1956; Lahde and Pahkala, 1974). Goo conducted a study in which he coated different parts of *Pinus thunbergii* seed with wax and placed them on the soil surface. Water was absorbed through any part of the pericarp not covered with wax at a rate that was nearly proportional to the area of seed coat in contact with the water. However, Hillel (1972) found that the rate of water absorption is not uniform over the entire seed coat. The permeability is greatest near the micropyle where the seed coat is generally thinner.

None of the previous experiments about seed-soil contact were conducted with jack pine but a depth of planting experiment has been conducted. Benzie (1965) conducted an experiment relating varying sowing depths to the germination of jack pine and several other species. He sowed seed in a fine loamy sand at 0, 0.5, 1.0, 1.5 and 2.0 cm below the surface. The seed were watered twice a week with sufficient water to approximate normal precipitation in Minnesota in the growing season. "Watering twice a week caused the soil surface to be alternately wet and dry, similar to conditions encountered in the field" (Benzie, 1965).

Benzie (1965) found the percent germination of surface sown seed to be 46%, for seed sown at 0.5 cm germination was 63% (not significantly different from the surface sown seed at alpha =0.05), for seed sown at 1.0 cm the germination was 8% and for seed sown at 1.5 and 2.0 cm germination was less than 8%. He concluded that 1) the critical depth for jack pine is between 0.5 and 1.0 cm, 2) covering the seed may be of questionable value, and 3) the optimum depth (below which seeding establishment is sharply curtailed) may vary under different growing conditions but the critical depth is more constant.

Experimental evidence indicates that seed-soil contact has a significant effect on water absorbtion and germination of seed. The critical factors are the seeds physical characteristics (i.e. seed size and seed

coat structure) relative to the particle size of the soil (soil texture). Again, soil texture must be considered when examining the effects of moisture stress on a particular tree species since the interaction of the seed and soil texture plays a role in water absorption.

2.8.4 MICROCLIMATE AND MICROTOPOGRAPHY

Microclimate and microtopography also have a very marked effect on germination. Harper et al. (1965) examined the effects of various artificial modifications of soil microtopography on the establishment of seedlings of several agricultural species. They found that the heterogeneity of the soil surface did in fact influence water uptake and germination of seed and that different species performed better under different conditions. The effect of microtopography is to protect the seed against water loss. This suggests that there are different and subtle requirements of different species for 'safe sites' and that variations in microtopography may influence species composition on a site (Harper et al., 1965). These variations may be explained by differences in relative humidity. Cracks in irregular soil surfaces provided sites with a higher relative humidity where the seeds were protected from excessive dessication (Harper and Benten, 1966).

2.9 WIND

The effects of wind on plants is a complex and extensive topic that will not be reviewed in its entirety. Several studies investigating the effects of wind on tree species are reviewed. For thorough reviews of the topic see Grace (1977), Grace (1981), Jones (1983) and Savill (1983).

Rees and Grace (1981) cite several sources which "...suggest that the effect of wind on plant growth and development are caused by wind-induced water stress...". They also note that this view has arisen from the dwarfed appearance of plants in droughty habitats and by the commonly held belief that transpiration is driven by the wind, even though there is ample evidence to the contrary. Wind can affect water status 1) by causing damage to the leaf surfaces from collisions between leaves; 2) by causing mechanical shock which makes the stomata open more widely or close somewhat; and 3) through mechanical stimulus, the leaf water potential might change directly, as in the motor cells of *Mimosa* (Rees and Grace, 1981). "Prolonged exposure to wind can also induce morphological and anatomical changes in plants" (Grace, 1977).

Wadsworth (1959) and Morse and Evans (1962) (both cited in Grace, 1977) found that there was an optimum wind speed for plant growth. Wadsworth (1959) conducted a wind tunnel study, using natural environmental conditions, with *Brassica napus* in sand culture. The results showed that the relative growth rate (RGR) was optimum at 0.7 m/s (2.5 km/hr) and was significantly reduced at 4.0 m/s (14.4 km/hr). Wind speeds used were 0.3, 0.7, 1.7 and 4.0 m/s (1.1, 2.5, 6.1 and 14.4 km/hr respectively). Morse and

Evans (1962) found almost the identical relationship. Maximum RGR of tomato (*Lycopersicun lycopersicon)* , *Medicago spp.* and *Trifolium spp.* was attained at 0.3 m/s (1.1 km/hr) and was reduced at 3 m/s (10.8 km/hr). Wadsworth (1960, cited in Grace, 1977) conducted a similar experiment as above but using solution culture as opposed to sand. He found no significant effect of wind speed on the RGR of the plant. Grace (1977) feels that the results of the sand medium experiments, when compared to the experiments with plants grown in liquid culture, "...are consistent with the view that the principal effect of wind... was to increase the rate of transpiration to a point where the supply of water from the soil did not keep pace with the rate of loss". In a soil medium there is hydraulic resistance; whereas, in a liquid the only resistance is within the plant.

In their study with *Pinus contorta*, Rees and Grace (1981) found that collisions between needles do not affect the cuticular conductance of the needles as it does in some other plant species. This is probably the result of the differences in leaf morphology between conifers and broad leafed plants. The light weight needles and the hard needle surface seem to reduce this kind of damage in conifers. Similar results were noted by Dixon and Grace (1984).

Shaking of plants has been found to affect growth (Rees and Grace, 1980b). Rees and Grace (1980a, 1980b) conducted studies investigating the effects of mechanical and natural shaking (imposed by wind speeds of 0.6 to 8.5 m/s (2.2 to 30.6 km/hr) in a wind tunnel) on the growth of two year old *Pinus contorta* seedlings. The results show that continuous shaking reduces extension of the terminal and lateral shoots by 21 percent and affects needle extension. Branching habit, apical growth and radial growth were not affected. There was also a 20 percent reduction in cell division and a smaller reduction in cell elongation.

The shaken plants were under less moisture stress than the controls. This may be the result of the larger size of the controls resulting in a larger leaf area which may result in more transpiration per unit of stem or volume of soil (Rees and Grace, 1980a). A further study suggests that the effects noted above were not caused by water stress (Rees and Grace, 1981). Research with other plant species shows that tactile stimulus such as handling and stroking may affect the rate of respiration or evoke the production of the growth substance ethylene (Rees and Grace, 1981).

Caldwell (1970) used a fully climatized wind tunnel for a study on the effects of high wind speeds on photosynthesis, transpiration and stomatal aperature of a deciduous (*Rhododendron ferrugineum*) and a coniferous (*Pinus cembra* L., Swiss stone pine) species. He subjected these species to a wind speed of 15 m/s (54 km/hr) and found that the stomata of the deciduous species decreased greatly in aperature. Consequently, transpiration and photosynthesis also decreased. Pine seedlings were virtually unaffected by the 24 hr exposure to high wind speeds. The stomata hardly reacted at all and transpiration was little affected. Photosynthesis was affected mainly as a result of a change in orientation of the needles.

Wind also had no affect on needle (stomatal) conductance of *Pinus contorta* (Rees and Grace, 1981). They cite several authors which "...also found that wind had no effect on transpiration rates and stomatal

conductances of spruce and pine, suggesting that this may be a general characteristic of conifers". Large variations in transpiration rate were observed between 2 year old seedlings of *Fraxinus americana* L. (white ash), *Acer saccharum* Marsh. (sugar maple) and *Pinus resinosa* Ait. (red pine) (Davies et al., 1974). "Transpiration in *Fraxinus* was increased by wind regardless of velocity, while wind decreased transpiration in *Acer* and had no significant effect on transpiration in *Pinus* (Davies et al., 1974). Wind speeds of 2.1, 3.4, 5.1 and 9.6 km/hr were used.

Wind is an environmental factor which is often cited as contributing to moisture stress in plants. The above information suggests that with conifers wind may have little effect on transpiration but may affect growth through mechanical stimulus. The effects of wind speed on transpiration are further discussed in the section below on evapotranspiration.

2.10 EVAPOTRANSPIRATION

The transpiration of plants and the evaporation of water from bare mineral soils are highly dependent on environmental conditions and on the physical factors of the plant and the soil; consequently, these factors are important in any experiment investigating the interaction of the plant and soil and the effects of this interaction on plant growth. Evapotranspiration is a complex topic which will not be presented here in its entirety. For thorough reviews see Monteith and Weatherley (1975), Turner and Kramer (1980), Kramer (1983) and Rosenberg et al. (1983).

When discussing transpiration and leaf temperature, Gates (1968) notes that a leaf is coupled to its environment through the flow of energy and that the flow of energy to and from a leaf must balance. The environmental factors which enter into the energy budget are radiation, air temperature, vapour pressure and wind speed (Gates, 1968). The plant properties which enter into the budget are the absorptance and emittance of thermal radiation by the leaf surface, the leaf dimensions and structure, and the internal diffusion resistance of the leaf. These properties interact in many ways to affect physiological processes in the plant.

Gates (1976) notes that certain conditions must exist for water to be transpired from the leaf to the environment. These conditions are 1) there must be water available, 2) there must be energy available to turn the water to vapour, and 3) there must be a water vapour gradient from the inside to the outside of the leaf to drive the diffusion process. These same conditions have been deemed necessary by Hillel (1982) for evaporation to occur from bare mineral soils. These conditions are influenced by the same environmental conditions which affect the energy budget of the leaf and by the physical properties of the soil which correspond to the physical properties of the leaf (i.e. the absorptance and emittance of the leaf and similarily the soil will affect surface temperature).

Wind is one of the influential factors affecting the energy budgets of a leaf or soil. As wind speed increases, turbulence increases, thereby reducing the boundary layer resistance over a surface. As a result,

the evaporation rate increases as the wind sweeps away the water vapour close to the evaporating surface (Jones, 1983) and the vapour pressure gradient (the difference in vapour pressure between two sources) steepens.

In plants it has been suggested (through the use of models and through experimentation) that an increase in wind speed can cause a decrease in transpiration (Gates, 1968; Campbell, 1977; Grace, 1981; Rosenberg et al, 1983). This decrease is not necessarily the result of increased diffusion resistance from the closure of stomata but the result of changes in the environmental conditions around and within the leaf. The main effect of the wind is to cool the leaf. Not everyone, however, agrees that this cooling is significant (Kramer and Kozlowski, 1979; Kramer, 1983).

The wind cools the leaf by reducing the boundary layer and bringing leaf temperature closer to air temperature. At lower temperatures the concentration of water vapour in air is less. As a result, the difference in the concentration of water vapour (vapour pressure) between the substomatal cavities and the air beyond the boundary layer is less and the driving gradient is reduced (Gates, 1968). With a smaller driving gradient, the diffusion rate of water molecules is lower (Grace, 1981). Seginer (1971) found similar trends when he modelled evaporation from soils.

This is a very dynamic system. Changes in wind speed affect the convection of energy to and from the leaf and the boundary layer thickness and hence the resistance. As a result, with increasing wind speed, sometimes transpiration will increase, sometimes it will decrease and sometimes it will remain the same, given the conditions experienced by the leaf at the time of the wind speed change (Gates, 1976). One must remember that with plants, these trends are based on the performance of single leaves. Conditions will change within plant canopies due to the effects of adjacent leaves and plants.

Gates (1968) based his suggestions on an energy budget analysis using models to simulate natural conditions. This trend has been proven experimentally by Yamaoka (1958), Drake, et al. (1970) and Dixon and Grace (1984). Drake et al. (1970) conducted his study with an agricultural species. Yamaoka (1958) conducted his study with *Cyrptomeria japonica* while Dixon and Grace (1984) used *Pinus sylvestris* L., *Quercus robur* L. (English oak), *Fagus sylvatica* L. (European beech) and *Sorbus aucuparia* L. (European mountain ash) in their studies. In all studies and for all species, given the conditions used, transpiration rates declined with increasing wind speeds. In the latter two studies the leaf-air temperature differences also declined. With *Pinus sylvestris* the leaf surface resistance (stomatal resistance) declined with an increase in windspeed from 0.25 to 1.0 m/s (0.4-1.6km/hr) then increased as wind speed increased to 5 m/s (8.0 km/hr) (Dixon and Grace, 1984). This response was attributed to mechanical limitations of the wind tunnel rather than a response to wind speed and the vapour pressure gradient.

Low wind speeds, under 1.1 mi/hr (1.8 km/hr) have the greatest influence on transpiration and leaf temperature (Gates, 1968). Gates also notes that these very low wind speeds are almost always present in nature and that the most common fluctuations occur between 1 and 3 mi/hr (1.6-4.8 km/hr). Grace (1977) notes that most of the time wind speed will be in the range of 0-1 m/s (0-3.6 km/hr).

Wind may not be as significant a contributor to moisture stress in tree seedlings as is generally believed. Growth reductions or seedling mortality may be the product of a number of environmental and biological factors of which wind may not be the major contributor. This is especially true for conifers. Transpiration of conifers appears to be affected less by wind speed than does transpiration of deciduous species. The use of various wind speeds in these experiments may therefore have more influence on the drying rate of the soil than on the transpiration rate of the jack pine germinants. It is recognized that by affecting the drying rate of the soil, the wind is indirectly affecting the transpiration rate of the seedling by influencing the availability of water to the seedling.

2.11 INDUCING WATER STRESS

In a recent symposium, Krizek (1985) presented a thorough review of the methods for inducing water stress in plants. These methods are briefly presented here.

"Methods for regulating water deficits in plant tissues are perhaps some of the most difficult of all environmental variables to control experimentally because of the dynamic nature of water in the plant and its surrounding substrate" (Krizek, 1985). There are four methods of inducing water stress in plants and each has its advantages and disadvantages (Krizek, 1985). They are; 1) withholding water from the soil or other substrate; 2) the use of osmotica (salt solutions); 3) the use of semipermeable membranes or other techniques to separate the soil and the osmoticum and 4) adjusting the height of a water column and/or the hydraulic conductivity of the soil.

The first two methods are the most commonly used. Heydecker (1962) used soil maintained at three gross soil moisture levels. He controlled evaporation by covering a set of pots and dryed the soil by passing a stream of air over the soil surface of another set of pots. Fraser and Farrar (1953a) manipulated conditions by shading, watering and planting at different depths and in different mediums. Harper (1977) discusses the use of a sintered glass plate and manometer assembly by which a range of tensions between 0 and 200 cm of water (0 to -0.19 bars) was maintained. Larson and Schubert (1969) germinated their seeds on paper towelling saturated with PEG-400 (polyethylene glycol) at concentrations that would provide 0, -3, -7, -11 and -15 bars moisture stress. Bonner and Farmer (1966) used osmotic solutions of d-mannitol to induce water stress on sweetgum seeds. Glerum and Pierpoint (1968) withheld moisture from red pine, white spruce and tamarack for periods of time corresponding to the time to reach -1, -6 and -15 atmospheres.

In water withholding studies soil is often used. The use of soil is advantageous because it permits a close simulation of the natural environment and because it permits a realistic evaluation of the effects of water stress on germination in the natural environment (Kaufmann and Ross, 1970). Additionally, the plant is free from any toxic effects of osmotic solutions. This method is also the most difficult to control because "The plant may experience gradual or rapid dehydration depending upon the choice of media, size

and type of container, and species and cultivar used" (Krizek, 1985).

Harper (1977) notes problems with several of the soil methods used to simulate water stress. Harper states that:

> ...an experimenter cannot at all readily maintain a soil at any steady state that is drier than field capacity. This problem is often forgotten by experimenters who think that by continually watering soil volumes to constant weight, they are assuring an evenly distributed water supply; in fact they are usually supplying surface roots with water at field capacity and leaving deeper roots in drought.

Harper also states that when using pressure membrane techniques (i.e. sintered glass plates, ceramic plate cells) water tension cannot be controlled in volumes of soil large enough to support a single plant let alone a community of plants. Collis-George and Sands (1962) also note some problems with the use of sintered glass discs.

> Seeds exposed on a sintered glass discs appear to be positioned geometrically to the source of moisture in a dissimilar manner to that in the field, where they are either surrounded by soil (and soil water) or embedded in the surface. The area of contact of the seed coat and the soil matrix will inevitably be less in the experimental system....

Larson and Schubert (1969) note that "The water potential of the soil near the surface of a root is usually lower than the measured value of the soil mass would indicate". This would also hold true for seeds germinating in a soil medium. Because of this phenomena, tree seed germinating in soil experience greater soil moisture stress than seeds in osmotic solutions at the same measured water potential (Parmar and Moore, 1968; Larson and Schubert, 1969).

Manohar and Heydecker (1964) note that because a set level of soil moisture stress is hard to maintain in soils, researchers have resorted to using osmotic solutions. Compounds such as PEG, NaCl, sucrose, mannose, dextran, mannitol and sorbitol have been used in the past but have, on occasion demonstrated toxic effects (Krizek, 1985). For the past 25 years, PEG has been the most widely used substrate (Krizek, 1985).

Berkat and Briske (1982) cite many authors who have used PEG solutions to satisfactorily simulate the effects of drought on seed germination. Larson and Schubert (1969) felt that PEG 400 was "... a suitable osmotic substrate to induce water stress". In their experiment, they experienced no toxic effects as far as they could tell. Kaufmann and Ross (1970) observed small differences between total germination between a PEG solution and soil; however, when germination rate is important, PEG did not accurately imitate what happens in soil. Germination was more rapid in the PEG solution than in the soil. Bonner and Farmer (1966) recognized that the use of osmotic potential may underestimate the effects of matric soil moisture stress. Berkat and Briske (1982) noted several disadvantages of PEG solutions. They experienced difficulties in maintaining the stability of the solution's water potential through time and had problems with fungal contamination.

Manohar and Heydecker (1964), and Kaufmann and Ross (1970) state that difficulties arise when placing a seed in an osmotic solution. Seedcoats that are not intact or not differentially permeable may allow the solute to enter the seed. If this occurs, the osmotic pressure gradient between the seed and solution is reduced, and the solution no-longer exerts a water stress equivalent to the matric water stress. There may also be toxicity problems depending on the type of osmotic solution used.

The development of the membrane technique to separate the osmotic solution from the soil (Kaufmann, 1969) was meant to be a compromise between the soil and the osmotic solution techniques. The soil is placed on a cellulose acetate membrane with an osmotic solution beneath. After several days, the water in the soil equilibrates, by diffusion, with the osmotic solution. Thus, a negative soil moisture potential is imposed on the soil. The apparatus is covered to prevent evaporation. The problem with the system is that the membrane lasts for 14 to 20 days, an insufficient length of time for some experiments (Krizek, 1985).

A relatively new technique developed by Snow and Tingey (1985) imposes moisture stress by changing the height of a water column. The plant roots are suspended in a rooting medium above a water column of known height. Different levels of moisture stress are imposed by changing the height of the water column and/or the hydaulic conductivity of the rooting medium (change medium texture) and thereby controlling the moisture potential at the root surface. Krizek (1985) describes several advantages of this system over the others.

2.12 WIND TUNNELS

2.12.1 APPLICATIONS

Low wind speed wind tunnels have often been used to study evaporation and transpiration from plants and soils. Most recently, Dixon and Grace (1984) used a closed circuit wind tunnel to study the effects of wind on the transpiration rate of plants. Davies et al. (1974) conducted a study, using a wind tunnel, to determine how different wind speeds affect transpiration and stomatal aperture of several tree species. Other examples of the use of wind tunnels include Barthakur (1975) who studied leaf temperatures under controlled environment conditions, and Macklon and Weatherley (1965) who examined the factors affecting plant water deficits. Wooding (1967) and Grace (1977) present excellent reviews of wind tunnel theory and of the applications of wind tunnels. Other references are Salter (1947), Bradshaw and Pankhurst (1964) and Pocock (1960).

2.12.2 THEORY

"Basically, a wind tunnel is a devise intended to provide a controlled flow of air through a test

region where experiments may be performed" (Wooding, 1968). With the addition of environmental control equipment, a growth chamber like device with air control is created. This controlled flow of air is required to produce uniform conditions over the experimental material placed in the wind tunnel.

Open fans do not provide the same uniform air velocity over test material as does a wind tunnel. Air movement from fans is very turbulent, with eddies and still air variably located within the fan's air path. In turbulence, air particles "... are observed to travel in randomly moving fluid masses of varying sizes called eddies; these cause at any point in the flow, a rapid and irregular pulsation of velocity about a well-defined mean value" (Vennard and Street, 1982).

In a wind tunnel, at low velocities, laminar flow is possible. Laminar flow is preferred because adjacent sheets of air slip past each other like playing cards in a deck, in essentially parallel paths without mixing. Thus, little turbulence exists and a uniform velocity is possible.

Air velocity is also more uniform in the flow direction along the wind tunnel. As air moves through the wind tunnel, viscous effects retard the air flow near its walls. This results in the creation of a boundary layer. In pipe flow for example, once the boundary layer is established, the velocity decreases towards the wall parabolically and the same velocity profile exists throughout the pipe length (Vennard and Street, 1982).

2.13 OSMOTIC PRIMING

Osmotic priming was originally developed by horticulturalists after they observed that wetting and drying of seed accelerated germination when compared to untreated seed. Heydecker (1973) presents an excellent review of the history behind the develpment of osmotic priming and Heydecker and Coolbear (1977) review the literature regarding osmotic priming and other seed treatments.

Osmotic priming or osmopriming is a seed treatment which can increase the germinative energy of seeds. The treatment involves soaking the seeds in an aqueous solution of high molecular weight and at a certain concentration and temperature. The soaking treatment permits close control of the rate of water absorption of the seed, allowing completion of all stages of germination to a point prior to radicle emergence (Heydecker et al., 1974; Heydecker and Coolbear, 1977). "The aim [of osmotic priming] is that all the seeds should be brought to the very edge of the germination precipice without actually going over it, so that when they are sown, germination is synchronized and instantaneous" (Heydecker et al., 1974).

The analogy of the principles behind the procedure are described well by Heydecker (1973). The protoplasmic membrane of cells is impermeable to large molecules; therefore, only water is able to enter the cell. Water will continue to enter the cell until the potential within the cell is in equilibrium with the potential of the priming solution. If the solution has a potential of -10 bars then the cells will have a potential of -10 bars. If this potential is too low for the germination process to proceed, then germination ceases until such time as higher potentials occur.

The above phenomenon is advantageous if the scatter between the time of sowing and the time of germination is wide (i.e. some seed in a seedlot germinate faster than others) (Heydecker, 1973). Because the seed cannot continue germinating after the potential within the cells is in equilibrium with the osmostic solution, the slower germinating seeds have an opportunity to 'catch-up' to the faster germinating seeds. Then when sown into optimum conditions, the seedlot will germinate more uniformly.

2.13.1 OSMOTIC PRIMING IN FORESTRY

Osmotic priming has not been used much with forest tree species (Fleming and Lister, 1984; Simak et al., 1984) but exhibits several potential advantages which foresters may be able to utilize. Primed seeds sown in cold soils tend to germinate faster than unprimed seeds. Fleming and Lister (1984) found that their best priming treatment decreased the germination time of black spruce (*Picea mariana* (Mill.) B.S.P.) seed sown at 10°C by 14 days when compared to other treatments. Simak et al. (1984) observed similar results with Scots pine, while Heydecker et al. (1974) observed similar results with agricultural and horticultural species. Because primed seeds germinate faster at lower temperatures, when compared to unprimed seeds, they are less prone to attacks by pests and diseases and may be better able to compete against weed species which may have germinated earlier. Primed seeds theoretically need little additional water to complete germination (extend a radicle) and therefore would better be able to take advantage of periods of optimum moisture conditions.

Osmotically primed seed also have a higher soil penetrability. Simak et al. (1984) buried primed and unprimed seed 5 and 15 mm below the soil surface. They found that the germination percent of the primed Scots pine seed was more than twice as high (approx. 80% after 21 days) at both sowing depths when compared to the untreated seed. A seed was considered germinated when the seedcoat or cotyledons emerged through the soil surface.

No research on the effects of osmotic priming on jack pine has been found. However, a study investigating the effects of wetting and drying on jack pine seed was conducted by Russo (1978). Germination percent was not significantly different between different treatments of repeated wetting and drying cycles of jack pine seed. Tests have also been made showing that conditions favouring a high moisture content in jack pine seed will give better germination results (Matte et al., 1964).

2.13.2 THE OSMOTICUM

The most common solute used for osmotic priming is Carbowax 8000 (formerly called Carbowax 6000, tradename of Union Carbide). The chemical name is polyethylene glycol (PEG) and according to Heydecker et al. (1974) has a number of important properties. First, it readily dissolves in water. Second,

it is a true osmoticum, that is, it has large molecules which do not pass readily into plant cells. Third, it is chemically inert and therefore permits prolonged contact with seeds without causing harm.

Low-molecular-weight compounds such as metabolically inert sugars (eg. mannitol) and salts (eg. KNO_3) have been used in the past but have been found to accumulate to harmful concentrations within cells (Bewley and Black, 1985). The only major advantage these compounds have over PEG is that they are less viscous than PEG and therefore do not interfere with oxygen uptake by seeds (Heydecker and Coolbear, 1977). Heydecker and Coolbear (1977) note that "...in PEG '6000', oxygen solubibity [sic] is 50% that of water and oxygen mobility is only 10%, depressing relative oxygen availability to the order of 5%...". No matter which compound is used, the seed must be protected from microbial attack or the proliferation of seed-borne pathogens.

2.13.3 THE PRIMING PROCESS

Bewley and Black (1985) note that priming treatments needed to optimize germination vary between and even within species and must be determined empirically. Two rules apply when determining an optimum priming time: 1) for any given osmotic potential, a longer priming treatment is required at lower temperatures, and 2) at a certain temperature, a longer priming time is required at lower osmotic potentials. For most seeds, the most effective range of osmotic potential is -5 to -20 bars and temperatures from 10-20^{o}C. Simak et al. (1984) treated Scots pine seed for 11 days in an -11.8 bar solution of PEG at 15^{o}C. They tried only one treatment level. Fleming and Lister (1984) tested several osmotic priming treatment levels. They found that the optimum treatments for black spruce were -12.5 bars at 20^{o}C for 14 days and -12.5 bars at 15^{o}C for 21 days.

2.13.4 STORAGE OF PRIMED SEED

The effects of storage of osmotically primed seed again varies between species. In agriculture and horticulture, the storage of osmotically primed seeds has resulted in a reduction in the advantages originally gained by priming (Gibbins and Heydecker, 1977; Heydecker et al. 1974). However, in forestry the reduction in germination energy is not as severe. Fleming and Lister (1984) stored dried, primed black spruce seed for 56 days at 0.5^{o}C with relatively little deterioration in germinative speed and vigour. Simak et al. (1984) experienced no reduction in germinative energy of dried, primed Scots pine seed. The seed were stored for two weeks at 0^{o}C in glass bottles and then sown singly in plant boxes of peat and stored at 4^{o}C for five weeks.

3.0 METHODS

3.1 INTRODUCTION

As mentioned in the introduction, the purpose of this reasearch was to observe the effects of moisture stress on the germination and initial development of jack pine grown on three soil-texture types. Two sets of experiments were conducted: 1) a germination study to observe the effects of moisture stress on germination, and 2) an ontogeny study to observe the effects of moisture stress on five stages of ontogeny. The experiments were conducted as pot studies in a controlled environment wind tunnel located in a greenhouse. This section begins with a description of the methods common to both the ontogeny study and the germination study. These are; the construction and operation of the wind tunnel; the environmental conditions within the wind tunnel; the collection and processing of the soil; the seed and seeding procedures in the experiments; and the definitions of seedling condition. The procedures unique to the germination study and the ontogeny study are then presented.

3.2 THE WIND TUNNEL

3.2.1 CONSTRUCTION

The wind tunnel (Figure 1) is a closed circuit type modelled on a wind tunnel designed by Weatherley and Barrs (1959) and modified by Macklon and Weatherely (1965). It produces an air stream of controlled speed, temperature and humidity.

The wind tunnel was constructed in three sections with "2x2" inch framing. Where additional reinforcing was required, larger dimension lumber was used. The test region of the wind tunnel was enclosed on three sides with clear plexiglass sheeting. The balance of the tunnel was covered with 10 mm plywood sheeting protected with white enamel paint. The plywood and plexiglass was secured to the inside of the framing members. Access to the test region was gained through plexiglass doors designed such that they could be sealed and such that a smooth surface was maintained within the wind tunnel. To reduce the heat load on the cooling equipment, the tunnel was covered on the outside with 5 cm thick styro-foam insulation placed between the framing members.

A refrigeration unit continuously cooled and dryed the air within the wind tunnel and thermostatically controlled heating elements cycled off and on to maintain the temperature near the set value. Humidity levels were maintained near the set values by atomizers controlled by a humidistat and

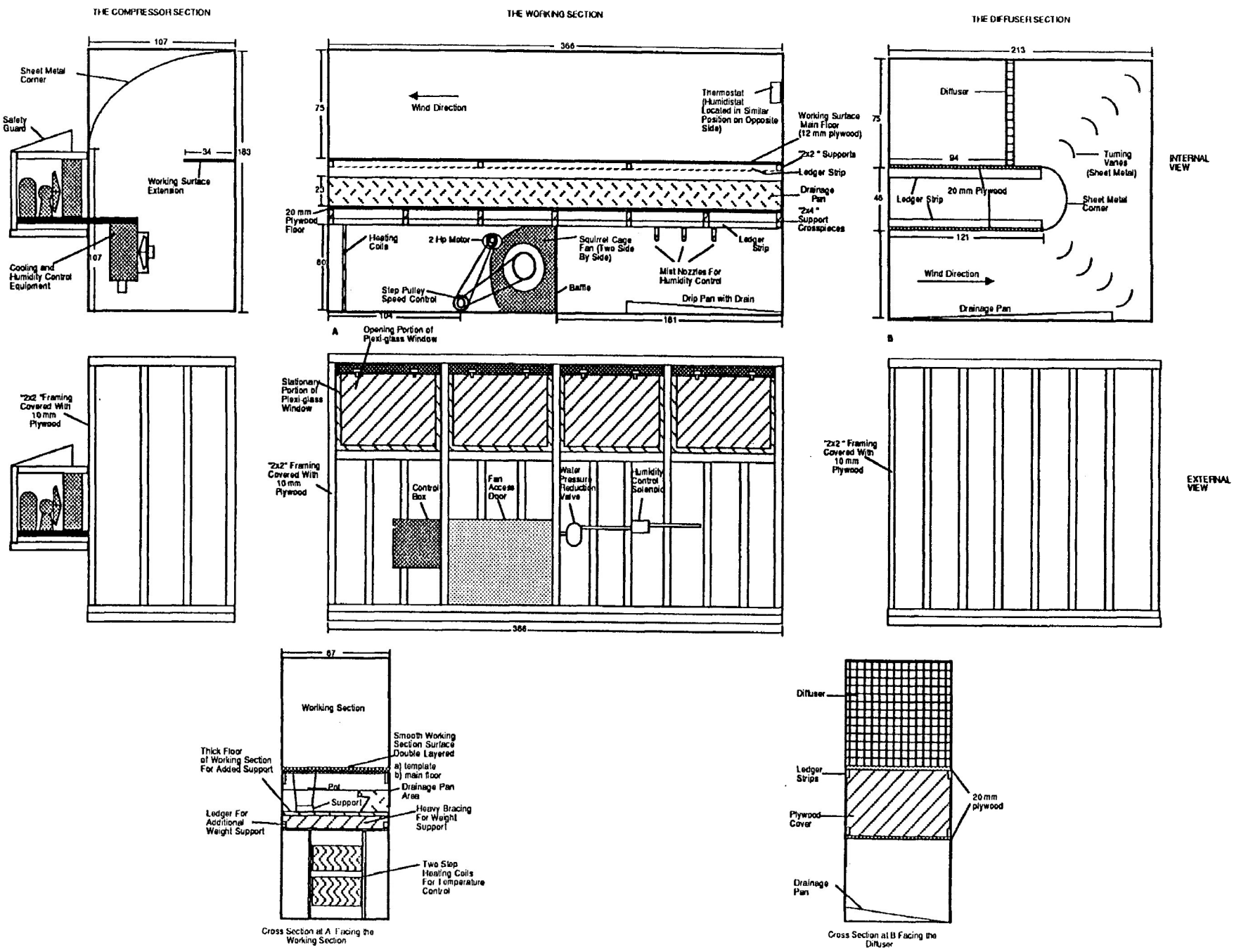


Figure 1. Schematic drawings of the wind tunnel showing the internal view, the external view and selected cross sectional views (in cm).

valve. The humidistat and thermostat were located immediately before the entrance to the test region. Once the sensing units were set, environmental control was automatic. Wind speed was adjusted by changing drive pulley ratios between the drive shafts of the motor and the fan. A 2 hp motor was used to drive two 30 cm diameter squirrel cage fans.

The test region of the wind tunnel is 3.6 m long and 1.25 m wide. It can accomodate material up to 75 cm high (above the working surface) and has a trough 40 cm deep beneath the working surface. The floor beneath the trough of the test region is well reinforced and can hold approximately 600 kg evenly distributed over the surface. With these dimensions, the test region was able to accomodate 84 pots 15 cm in diameter. The trough was isolated from the rest of the wind tunnel in order to prevent air movement into the trough and evaporation from the soil through the bottom of the containers.

In order to minimize turbulence, the working surface of the wind tunnel should be as flat and uniformly textured as possible. To accomplish this, the bulk of the pots extended beneath the working surface into the trough. The rim of the pot protruded above the working surface. A template, the same thickness as the rim of the pot, was constructed and placed over the pots. With the template in place, and the pots filled to the brim with soil, a smooth, relatively even surface was produced. Figure 2 shows the pot layout for the main floor and template.

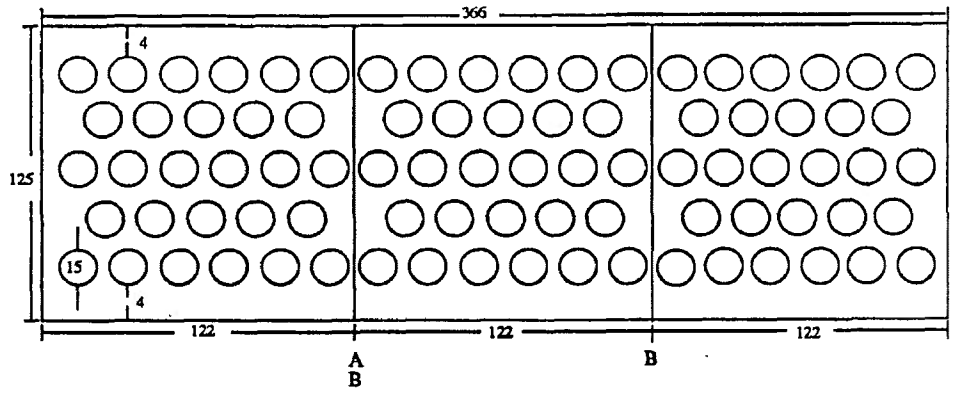


Figure 2. Working surface main floor and template layout of pots in the wind tunnel. The main floor was in two sections whereas the template was in three sections. A. Main floor division point. B. Template division point. All measurements in centimetres.

The entrance of the test region contains a screen to serve as a flow straightener. This device also cuts eddies, if present, into smaller eddies which dissipate as they enter the test region of the wind tunnel. The screen was constructed from four egg-crate plastic panels, glued together in pairs, with window screening glued between one pair of the panels. These panels are usually used as diffusers for fluorescent light fixtures.

When the wind tunnel was in the planning stages the maximum air speed attainable, given the equipment used, was unknown. The design criteria for the wind tunnel was a maximum wind speed of 15

km/hr. Higher wind speeds were not required since average wind speeds measured in the field 10.1 m above the soil surface, from April to August in the Thunder Bay, Ontario area did not exceed this value (Anonymous, 1982c). Once the wind tunnel was constructed and in operation, several trial runs were conducted. The results of the trial runs indicated that the original design could not produce the required maximum wind speed. After several modifications, a maximum speed of 12.8 km/hr was attained. To evaluate the performance of the wind tunnel, air velocity was measured 3, 10 and 20 cm above the working surface at 17 and 31 cm intervals along the width and length respectively.

3.3 ENVIRONMENTAL CONDITIONS

In the wind tunnel, air temperature alternated diurnally from 25^{o} C during the day to 13^{o} C at night. These temperatures approximate the Canadian Climate Normals (Anonymous,1982b) for the mean maximum and minimum July temperatures for four land stations in and around Thunder Bay. Relative humidity alternated from 55 % during the day to 60 % at night.

Radiation was limited to levels encountered in the greenhouse during the experiments. Two 40 watt fluorescent tubes per 1.25 m length of test region of the wind tunnel provided supplemental lighting to maintain a 17 hour day length.

According to the Canadian Climate Normals (Anonymous, 1982c), mean May, June and July wind speeds, measured at 10.1 m above the soil surface in the Thunder Bay area are 14.7, 12.4 and 11.6 km/hr, respectively. These wind speeds cannot be considered indicative of wind speeds found at the soil surface. Wind speeds at the soil surface vary with microtopography, surface texture and vegetative cover. These factors contribute to the creation of a boundary layer which results in a gradual decrease in wind speed the closer one moves to the soil surface.

The use of wind in these experiments was to model, as well as possible in laboratory conditions, the natural drying processes which occur in the field. Three wind speeds were selected such that three distinct drying rates would be produced. The actual wind speeds used were very much the result of mechanical and physical limitations of the wind tunnel.

The means of the three wind speeds used in the experiments were 4.0, 6.7 and 10.9 km/hr. These means were determined by measuring the wind speed at 15 cm intervals along the length and 3 cm above the working surface in the centre of the working section of the wind tunnel. During the experiments, the test wind speeds were maintained for 16 hours during the day, and reduced to 2.5 km/hr at night. The diurnal fluctuations were used to simulate field conditions.

To allow for the possibility of water conductance from the deeper soil layers to the soil surface, round pots 20 cm deep, 15 cm in diameter and 4 l in volume were used. Three soil texture types were used to allow for variations in conductance associated with textural changes.

3.4 SOIL

The experiments were conducted on three soil texture types characteristically associated with jack pine in northwestern Ontario. These soil types were 1) a sand 2) a loamy sand and 3) a sandy loam. Field areas of these soil types were located in the spring of 1984 within the vicinity of Thunder Bay, Ontario. All samples were from outwash areas.

3.4.1 COLLECTION AND INITIAL PROCESSING OF SOIL

When the desired soil types were located, the duff and Ah horizons were removed, and the soil of the B horizon excavated to a maximum depth of 20 cm. The purpose of removing the Ah horizon was to reduce the amount of organic matter in the sample. Organic colloids hold moisture and nutrients differently than do mineral soil particles and the different soil types and locations have varying depths of Ah. If this horizon was mixed with the mineral soil, then the soil properties could have changed, over time, as the organic matter decomposed. Consequently, comparisons of results for the same soil type between different wind speed tests could have been more difficult. Each soil type was thoroughly mixed to ensure uniform conditions throughout the soil sample and sieved through a 1/4 in (6.4 mm) mesh to remove any roots and large stones.

Soil texture, pH, and concentrations of exchangable cations (N, P, K, Ca, Mg) were determined. The chemical analysis was conducted by Agri-food Laboratories in Guelph, Ontario. Soil moisture depletion curves were constructed using a pressure plate apparatus. The depletion curves were used to relate soil moisture content (%) to soil moisture potential (bars). In this paper, moisture content (%) is always expressed on a dry weight basis.

The hydraulic conductivity of saturated soil was determined using the procedures described by Bowles (1978) and Klute (1965). A compaction permeameter and the falling head method were used.

3.4.2 CONTAINER REFILLING AND ASSOCIATED METHODOLOGY

Before either the ontogeny or the germination tests began, the soil of a particular soil type was passed through a 1/4 in (6.4 mm) screen and mixed in a small cement mixing machine. This procedure ensured that soil texture and moisture content was uniform throughout the soil mass and that any large, dry lumps of soil were broken.

When the pots were repacked, they were brushed out to remove any residual material from the previous run, a piece of paper towel was placed in the bottom of the pot and the pot filled until the soil was mounded 5 to 10 cm above the pot rim. Each pot was lifted and dropped a distance of 5 cm, three times. The soil was then levelled off to the rim of the pot.

Four pots were processed as above and weighed. To ensure a high bulk density and thus reduce the amount of settling below the rim of the pot after wetting, the highest weight of the four pots was used as the standard that all other pots must reach. If this weight was not reached, more soil was added to the pot and the pot dropped and weighed repeatedly until it reached the set weight. This procedure was conducted to ensure that all the pots of a particular soil type within a run had approximately the same bulk density.

Bulk density is a critical factor governing the drying rate of soils. Before the above procedure was followed, I found that pots with a similar soil type but different bulk density did not dry at the same rate when placed in the wind tunnel and subjected to the same wind speed. Hence it was essential that the above procedure be used in order to attain consistent bulk densities for all pots.

Once all the pots of all three soil types were processed, they were placed in trays of water, one soil type at a time, for one hour. The pots were also watered from above with a gentle stream of water. Five randomly selected pots were weighed and a minimum allowable weight per pot was determined. The minimum allowable weight was the highest weight of the five pots unless this weight was subjectively judged higher than the weights of the other four pots. The weights of the five pots were usually similar. Pots not attaining the minimum allowable weight were watered from above until they reached this weight. This procedure ensured that the soil was thoroughly saturated before the run began. Two complete lots of soil were available. When one experiment was under way in the wind tunnel using one lot of soil, the second lot of soil was being processed for the next run in the wind tunnel.

If the pots were being used for the germination study, they were randomly numbered and placed in the appropriate location in the wind tunnel. The experiment did not begin until 24 hours after the last set of pots were processed in order to allow soil moisture to equilibriate within the pots. If the pots were being used for the ontogeny study, they were placed randomly on a bench in the greenhouse and sown. Further pot handling procedures are given in the Ontogeny Study and Germination Study sections.

3.4.3 SOIL MOISTURE CONTENT AND BULK DENSITY DETERMINATION

During the experiment, soil moisture content was determined gravimetrically for the 0-1, 1-2, 2-4, 4-6, 6-8, 8-10, 10-12 and the 12-14 cm depth in each sample pot. Soil samples were taken from several pots, of each soil type, at each sample time, as required in each individual experiment.

Soil samples from the 0-1 and the 1-2 cm depths were collected by scraping the soil surface with a scoopula. The other depths were sampled using a 1.5 cm diameter glass tube graduated in 2 cm intervals. Soil sample extraction holes were refilled with a plug of soil, extracted with the glass cylinder. The plug of soil was taken from pots designated for this use. The holes in the soil sample refill pots were plugged with cork or rubber stoppers.

During the experiment, the soil temperatures of the 0-1 and 2-4 cm depth of each soil type was measured using thermocouples and a multi-channel recorder. Temperature probes were installed in

randomly selected soil sample refill pots of each soil type for some runs of the experiment.

To compare soil types between wind speed runs, the same sampling times were required. Because the soils dryed at different rates at different wind speeds, they were sampled at different times. To obtain data for similar sampling times, the actual moisture content data were graphed and the soil moisture content percent interpolated at the same times for all soil types at all wind speeds. The interpolated data were used in the analysis.

The soil moisture content in percent and the soil moisture depletion curves were used to determine the soil moisture potential reached at each sample time. Graphs showing the change in soil moisture content and potential, with depth, over time, were drawn. With these graphs, the drying characteristics of each soil were determined at each wind speed and the wind speed runs compared.

At the end of each run of the experiments, soil bulk density was determined for all undisturbed soil sample refill pots. The 0-9 and the 10-20 cm soil depths of each pot were sampled. Two samples were taken per depth.

3.5 SEED AND SEEDING

3.5.1 SOURCE

The seed was collected in Geraldton district in 1981 by the Ontario Ministry of Natural Resources. The source is Hills site region 3W (Hills, 1959), Ontario Seed Collection Zone 3400. A large supply of this seed was available and this seed was used for all tests. The seed had a germinative capacity of 98 %.

3.5.2 SOWING AND SPACING

When seed was sown in either the ontogeny or the germination study, a template was used to locate fifteen seed spots accurately in each pot (Figure 3). Seed were spaced 2 cm apart within and 1.5 cm between rows, and offset 1 cm between adjacent rows. Only one half the pot was sown, the other half was used for periodic soil sampling. A buffer row of seed was sown around the 15 sample seed spots. Seed were pressed down even with the soil surface to provide consistant seed-soil contact in all the experiments.

3.6 DEFINITIONS OF SEEDLING CONDITION

Because there were few seedlings and due to the nature of measurements conducted on the seedlings, a destructive sampling technique could not be used to determine seedling condition during the experiments. Consequently, a visual method of seedling condition classification was developed and used. The following definitions were used.

A germinant was considered dead when the radicle had dryed and turned brown. A seedling was considered dead when the most recently formed epicotyl leaves had turned an ash green colour and when the hypocotyl had contracted and twisted. A seedling was classed as wilted when the inner whorl of epicotyl leaves appeared normal but the cotyledons and hypocotyl were wrinkled and slightly twisted respectively. A preliminary test was conducted to determine when the seedlings would revive after they had reached certain visual levels of drying, i.e. the ash green colour. As long as the inner whorl of epicotyl leaves appeared normal, regardless of the condition of the larger, outer whorl leaves (epicotyl and cotyledons) most seedlings would revive after being rewatered.

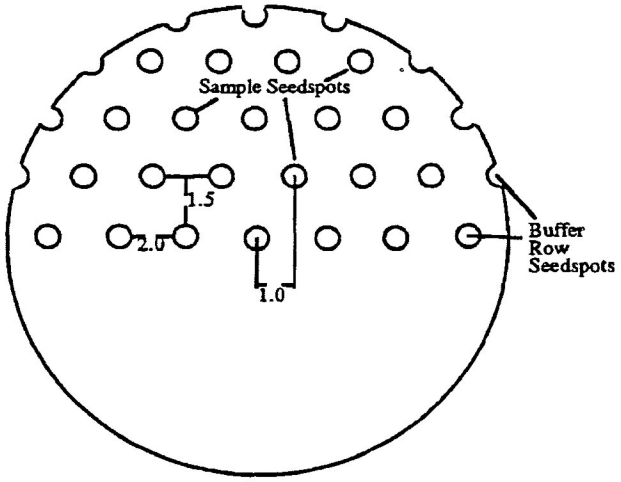


Figure 3. Seeding template used to locate 15 sample seedspots accurately in each pot. Template diameter is 15 cm. Balance of pot area was used for soil sampling. All distances are in centimetres.

3.7 OSMOTIC PRIMING

3.7.1 APPARATUS

The seed was osmotically primed using an apparatus (Figure 4) designed by Mr. M. Adams, a technician at the Great Lakes Forestry Centre. The apparatus consisted of a leveling bulb used as the priming vessel, with the wide opening end facing upwards and fitted with a one hole rubber stopper. To prevent large changes in the concentration of the osmotic solution, a condenser unit was fitted into the one hole stopper to condense any water vapour leaving the solution. Continuously running cold water from a tap was used for cooling in the condenser. The top of the condensing tube was plugged with glass wool to allow air movement while reducing the chance of contamination from air borne pathogens. The bottom end of the leveling bulb was tightly packed with glass-wool to prevent the seed from sliding into plastic tubing connected to a compressed air line. The osmotic solution was aerated by bubbling

compressed air through the solution. Sufficient air pressure was used to keep the seed continuously moving in the osmotic priming medium.

The leveling bulb and condensing unit were attached by clamps to a support stand. This assembly was lowered sufficiently into a 4 L Griffin beaker of water such that the leveling bulb was completely immersed. A Lauda refrigerated circulator was used to keep the water in the Griffin beaker at a constant temperature of 15° C for the priming treatment. Several tests of the apparatus, using water instead of the priming solution, were conducted to be certain that the apparatus would function properly during the experiments.

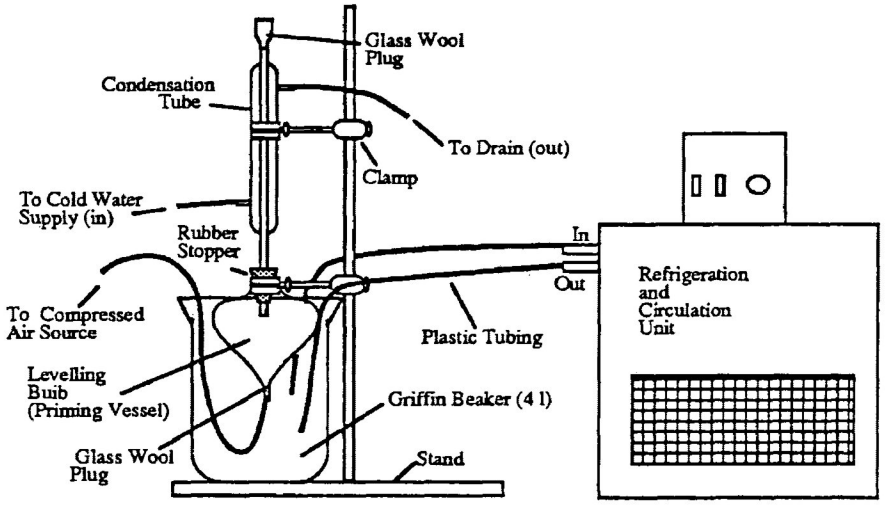


Figure 4. Diagram of osmotic priming apparatus.

Polyethylene glycol (PEG) 8000 powder (Fisher Scientific Carbowax PEG 8000, Formerly PEG 6000) was used as the osmotic solution. A stock solution of -12.5 bar osmotica was mixed on a heating magnetic-mixer before the start of the three priming runs. The mixing rate, determined from Michel and Kaufman (1978), was 338.1 g of PEG 8000 to 1050 ml of distilled water.

The selection of the osmotic solution temperature and concentration was extrapolated from the experimental results with Scots pine and black spruce of Simak et al. (1984) and Fleming and Lister (1984) respectively. A proper test to determine the optimum osmoticum concentration and temperature for jack pine was not conducted due to the magnitude of such an experiment and to time constraints.

3.7.2 DETERMINATION OF PRIMING DURATION

Prior to running the wind tunnel germination tests with the osmotically primed seed, a preliminary priming and germination test was conducted to determine the duration of priming required. The priming vessel was filled with 350 ml of -12.5 bar (PEG) solution and 9 g of surface sterilized jack pine seed. The seed were sterilized by soaking in a 10 percent Javex solution for 10-15 seconds and rinsing with distilled

water. The seed were padded dry before being placed in the priming vessel. The apparatus operated 24 hours a day with the laboratory lights on for 16 and off for 8 hours each day. At the termination of the priming run, the osmotic solution and the seed were poured through a strainer. The seed were transferred to a large beaker and rinsed repeatedly in distilled water. The seed were then scattered on sheets of paper towel and allowed to air dry for 24 hours at room temperature.

Ideally, to determine if the seed have been primed to the maximum limit, the seed should be left in the priming solution until their seed coats begin to crack. In this study, the seed coats had not cracked after 22 days in the solution. To save time, it was decided to terminate the osmotic priming treatment and use the 22 day period in all subsequent treatments.

A growth chamber germination test was conducted to determine if the osmotic priming treatment was successful and if seedling development was affected in any way by osmotic priming. Four randomly selected lots of 50 osmotically primed and control seed were placed in filter paper lined petri dishes, watered and placed in a plastic bag covered tray in a growth chamber at 20^{o} C days and 10^{o} C nights for 16 and 8 hours respectively. Germination was recorded daily. The germinated osmotically primed seed were removed from the petri dishes and planted in a peat Vermiculite mixture to determine if these seedlings would develop normally. Osmotic priming had no apparent effect on the germinants.

3.8 GERMINATION STUDY

The purpose of the germination study was to determine the effects of negative soil moisture potential on the germination and subsequent growth of jack pine. Seed were sown at various soil moisture potentials and the effects on germination and initial growth observed. The study was divided into two sections: 1) the soil drying study, and 2) the germination study.

The purpose of the soil drying study was to determine the drying characteristics of each soil texture when subjected to the three wind speed treatments. This information was required to determine when the soil reached specified soil moisture potentials at which time seed would be sown.

In brief, the germination study consisted of sowing seed on three soil texture types at several soil moisture potentials. The drying rate of the soil was varied by the use of three wind speed treatments. The germination rate of the seed was monitored. Unfortunately, no seed germinated on the soil surface in the wind tunnel. To check seed viability, the ungerminated seed were removed from the soil surface, placed in petri-dishes and placed in a growth chamber under controlled conditions. Germination was monitored.

The germination study was repeated twice since in the first attempt seed did not germinate in the wind tunnel. For ease of presentation and discussion, the first attempt of the germination study is called the preliminary germination study and the second attempt the main germination study. The original study plan was modified to accommodate unanticipated problems. In the preliminary germination study (the first attempt), the soil did not dry at the rate determined by the soil drying study. Therefore, the means of

determining when the soil reached specified soil moisture potentials was changed for the main germination study (the second attempt). Additionally, for the preliminary germination study, seed did not germinate on the soil surface in the growth chamber. After removing the seed to petri-dishes and a growth chamber to check the viability of the seed, it became apparent that when compared to controls (seed taken from storage), the wind tunnel sown seed germinated faster in the petri-dishes than controls. This effect was similar to what is observed with osmotically primed seed. As a result, a second seed treatment (osmotically primed seed) was added to the main germination study. The main germination study was conducted with the modifications.

The details of the soil drying study and the preliminary and main germination studies are presented below. The preliminary and main germination study procedures are combined under THE GERMINATION STUDY heading.

3.8.1 THE SOIL DRYING STUDY

Because seed had to be sown at specific soil moisture potentials, a soil drying study was conducted prior to the germination studies to determine the time required for each soil type to reach the specified soil moisture potentials at a given wind speed. The pots were filled and treated as specified in the Soils section and placed in the wind tunnel. No seed was sown. Soil samples were taken periodically, following the procedures described in the Soils section, until the surface centimetre of soil had reached the final desired soil moisture potential. Soil drying curves were constructed from these data, for each soil type, and the time required to reach the specified soil moisture potentials determined. The soil drying study was to provide a base on which to determine the sowing times in the germination study. Unfortunately the procedure did not work as planned. Details are presented below in section 3.8.2.1.

3.8.2 THE GERMINATION STUDY

3.8.2.1 PROCEDURES

In the study plan, untreated seed were to be sown when the 0-1 cm soil depth of each soil type was saturated and at soil moisture potentials of -0.5, -1.0, -2.0, -4.0, and -6.0 bars. The pots were filled and treated as outlined in the Soils section. Untreated seed were sown using the procedures outlined in the section on Seed and Seeding. Seed were removed from cold storage one hour prior to sowing. Only one seed was sown per spot. Soil moisture content was periodically determined as outlined in the Soils section.

After starting the germination experiment at the moderate air speed, it became apparent that the study plan methods could not be followed precisely. The soil was not drying at the same rate in the

preliminary germination study as it did in the soil drying study. Because of this, seed were sown when the 0-1 cm soil depth was saturated and at no other time. The sowing times determined from the soil drying study could not be used. Similar results were observed in the low air speed run. It became evident that some modifications to the study plan were required. These modifications would subsequently become the procedures for the main germination study (the second attempt of the germination experiments).

The soil moisture content curves were graphed for both the soil drying study and the preliminary germination study. The graphs showed that although curves from the two studies were not identical, they did closely parallel each other. This trend was verified when the soil moisture content curves from the ontogeny experiments were also graphed. It was hypothesised that this parrallelism could be used to predict the drying curve for the second attempt of the germination study (the main germination study). To determine the proper sowing times for the main germination study, the initial soil moisture content of a wind speed run was determined immediately after the pots were placed into the wind tunnel and a projected soil moisture content curve drawn parallel to the other curves. The initial soil moisture content was used as a starting point for the projected soil moisture content curve. Sowing times were then determined from the projected curve.

In the preliminary germination study, seed sown when the soil was saturated did not germinate in the wind tunnel. The experiments were terminated when the soil surface appeared dry and it became evident that no germination would occur. A test was conducted to determine the viability of the ungerminated seed. The ungerminated seed, excluding buffer row seed, were removed from the soil surface and placed in white filter paper lined petri-dishes. These petri-dishes plus a set of controls, seed taken from cold storage, were watered and placed into a plastic bag covered tray in a growth chamber. Environmental conditions in the growth chamber were 24 °C days and 16 °C nights for 14 and 10 hours, respectively. The control consisted of four replications of 50 untreated seed each. Seed were considered germinated when the radicle was greater than 2 mm long. Germination was monitored daily. Seed not germinating in the growth chamber were dissected to determine if they were sound.

The growth chamber germination test results showed that the germinative energy of the seed sown in the wind tunnel in the preliminary germination study was greater than the germinative energy of the control seed. A similar response is observed when osmotically primed seed are compared to unprimed seed. The methods used in the second attempt of the germination study (the main germination study) were modified to include untreated seed and osmotically primed seed. It was hypothesized that the osmotically primed seed would germinate in the wind tunnel since they were being placed into the wind tunnel in a state of advanced germination similar to those seed that were removed from the soil surface in the previous run.

In the preliminary germination study, seed sown on saturated soil failed to germinate in the wind tunnel at the low wind speed. If they did not germinate when the soil was saturated then they would surely not germinate if sown when the soil was at lower soil moisture potentials. Therefore, the number of

sowing times in the main germination study were reduced. Seed were sown when the 0-1 cm soil depth was saturated and at soil moisture potentials of -0.5 and -1.0 bars. Additionally, since treated seed were also being tested, the number of sowing times would have to be reduced to provide sufficient pots to run the new treatments.

The revised methods for the main germination study are as follows. Prior to each run of the wind tunnel, seed were osmotically primed as described in the Osmotic Priming section. The wind tunnel germination test began 24 hours after the seed were removed from the priming solution. The soil was treated and the pots filled as described in the Soils section. Osmotically primed and untreated seed were sown using the procedures outlined in the section on Seed and Seeding. Seed were sown when each soil type was saturated and at soil moisture potentials of -0.5 and -1.0 bars. Only one seed was sown per spot. Soil moisture content was periodically determined as outlined in the Soils section. Between sowing times the seed were stored in an air tight plastic container at 2°C.

Seed were observed daily for any signs of germination. The experiments were terminated when the soil surface appeared dry and it became evident that no germination would occur. The same procedure as above was used to determine the viability of ungerminated seed except that environmental conditions in the growth chamber were changed to 25°C day and 13°C night for 16 and 8 hours, respectively. The control in the main germination study consisted of untreated and osmotically primed seed.

3.8.2.2 EXPERIMENTAL DESIGN AND ANALYSIS OF DATA

Seed did not germinate on the soil surface in the wind tunnel in either of the two germination tests. All germination percent data is based on the petri-dish/growth chamber seed viability tests. Cumulative germination percents were determined for each soil type and wind speed treatment combination and for the control. Germination percent was calculated on the basis of the total number of filled seed in a replication. Soil moisture potentials could not be predicted accurately; as a result, the data for only the saturated soil moisture potential treatment were used.

In the preliminary germination study, no statistical analysis was conducted on the germination data, but graphs of percent germination versus time were drawn. Qualitative interpretation of graphical and tabular results was conducted. The soil moisture depletion curves were also drawn for each soil type in each wind speed run.

The main germination study was a split plot factorial design with wind speeds as main plots and the 2x3 factorial combination of seed treatment and soil type respectively as the subplots. There was no replication at the whole plot level and three replications at the subplot level. Because there is no replication at the whole plot level and because there is a restriction on randomization at this level, there is no statistical test for differences between wind speeds.

Three analyses of the data were conducted. Data were recombined for some of the analyses.

Germination percent was computed for each treatment combination. Graphs of percent germination versus time were drawn for several combinations of soil type, sowing time and seed treatment. An ANOVA was conducted to test for germination percent differences between treatments at several times from the start of the growth chamber germination tests. ANOVA's were conducted with all three wind speeds combined and for each individual wind speed. See Appendix A for the linear model and the expected mean squares table for this analysis.

To compare the germination values of primed and unprimed seed sown in the wind tunnel to the primed and unprimed control seed (seed taken from cold storage), the data within each wind speed treatment were analyzed as a oneway ANOVA. The combination of each soil type and seed treatment were treated as an individual treatment effect. Three soil types by two seed treatments results in 6 treatments. This plus the two seed treatment controls (primed and unprimed) summed to eight treatments tested in the oneway ANOVA. See Appendix A for the linear model and the expected mean squares table for this analysis.

A separate ANOVA was used to test for differences between the lots of control seed. There were three lots of seed, each lot consisting of the seed primed for each wind speed run and the untreated seed removed from cold storage. The analysis was conducted as a split plot design with lots as the whole plots and seed treatments and appropriate interactions as the subplots. See Appendix A for the linear model and the expected mean squares table for this analysis.

To test the assumptions of the ANOVA's, the data were graphically tested for homoscedasticity (constant variance) and normality, and transformed as required. Where means are given in the text, values are based on actual data. Tukey's (1953) HSD method was used to test for differences between transformed means. The soil moisture potential for the 0-1 and the 1-2 cm depths were graphed for each wind speed treatment.

All tests of significance were conducted at the 5 % level of confidence.

3.9 ONTOGENY STUDY

The purpose of the ontogeny study was to determine the effects of negative soil moisture potentials on the growth and development of jack pine at five stages of ontogeny. Each ontogeny stage was established on each of three soil texture types. Table 1 provides a description of the five ontogeny levels.

The experiment consisted of placing all five ontogeny stages of jack into the wind tunnel at the same time and subjecting them to three wind speed treatments. In the wind tunnel, only one wind speed could be run at a time. Height growth and germinant mortality were monitored during the wind speed treatment. When approximately 50 percent of the germinants in a treatment combination were dead and or wilted, the treatment combination was harvested. Shoot and root length and dry weight at time of harvest were determined. Soil moisture potential was monitored throughout the experiment. These values were converted to soil moisture potential from curves produced using the pressure plate apparatus on the three

soil texture types.

In order to place five stages of ontogeny into the wind tunnel at one time, a preliminary study was conducted to determine what interval the seed should be sown. This interval would be a function of the time required for the germinants to reach the five ontogeny stages. For example, ontogeny stage five would be sown first because it takes the germinants the longest time to reach this stage. Ontogeny stage four would be sown next because it takes germinants the second longest time to reach this stage. This study determined the time interval between sowing the stage five germinants and the stage four germinants and so on. This procedure is described below under the heading Germination Timing Study.

Table 1. Description of the five stages of ontogeny used in the experiment.

Stage	Description
1.	From the time when the seed coat is cracked to the time when the radicle begins emerging from the seedcoat (radicle length less than 2 mm).
2.	From the time when the radicle begins to penetrate into the soil to the time when the seed is slightly elevated with the hypocotyl bent.
3.	From the time when the hypocotyl is straight to the time when the cotyledons are just beginning to show beneath the seed coat.
4.	From the time when the cotyledons are spread apart but attached at the tips by the seed coat to the time they are fully released from the seed coat, one or two may remain attached.
5.	Beginning of epicotyl development: the epicotyl is longer than 2 mm.

3.9.1 GERMINATION TIMING STUDY

To observe the effects of soil drying on the five ontogeny stages, all five ontogeny stages of jack pine needed to be placed into the wind tunnel at the same time. Prior to the start of the experiments, a preliminary study was conducted to determine the time required for the germinants to reach the five ontogeny stages on each soil type. This entailed filling the pots as outlined in the Soils section, sowing one seed per spot, as outlined in the Seed and Seeding section, and observing the number of germinants reaching a specific stage of development each day after sowing. The pots were located randomly on a greenhouse bench. The greenhouse temperature was 23^{o} C during the day and 15^{o} C at night for 16 and 8 hours, respectively. The 16 hour photoperiod was supplemented with high pressure sodium lights. Humidity and temperature conditions were recorded continuously throughout the trial. Pots were watered daily, with water at room temperature, to ensure that the soil remained saturated.

To obtain the germination times, the preliminary trial was repeated twice with two pots per soil type. One other trial was rejected because of variable germination and soil drying between pots. In

subsequent trials, the bench was modified to eliminate these problems. The same environmental conditions and procedures as above were used during experimental runs to ensure similar timing of germination.

From the preliminary trial, the time required to reach each ontogeny stage (ontogeny time) and the difference between ontogeny times was determined (Table 2). The difference between ontogeny times was used as a time interval between sowings of each consecutive ontogeny stage. For example, it takes four days longer for the seedling to grow to ontogeny stage five than to ontogeny stage four (21 and 17 days for stage 5 and stage 4 respectively). Ontogeny stage five would be sown first and ontogeny stage four sown four days later. In this manner a sowing interval was developed. If seed were sown at this interval, then all five ontogeny stages could be obtained at the completion of the last interval. The sowing interval was similar for all three soil types.

3.9.2 ONTOGENY STUDY PROCEDURES

Before sowing, the pots were filled with soil as described in the Soils section, labelled, randomly numbered and placed in the numbered location on the greenhouse bench. Seed were sown following the procedure in the Seed and Seeding section and using the sowing interval determined in the germination timing study. Two seed were sown per spot to ensure a seedling at each spot. After germination, the seedspots were thinned to one germinant per spot. Of the two germinants, the one not at the same stage of development as the majority in the pot was removed; otherwise, one seedling was randomly selected for removal.

Table 2. The period of time from sowing required for the seedlings to reach the five ontogeny stages and the sowing interval (the time interval between sowings of consecutive ontogeny stages). Ontogeny stage five was sown first.

Ontogeny Stage	Time to Reach Ontogeny Stage (days)	Sowing Interval (days)
5	21	4
4	17	5
3	12	4
2	8	2
1	6	

When the germinants were ready to be placed in the wind tunnel, all the pots of one soil type were again placed in trays of water and allowed to stand for one hour. Five randomly selected pots were weighed. To ensure that the soil in all pots was saturated, the highest weight of the five pots was used as a minimum weight that all other pots must reach. Pots not attaining the minimum weight were watered

from above until they reached this weight. All pots were randomly numbered before being placed in the appropriate location in the wind tunnel. A twenty-four hour period elapsed before the experiment began in order to allow the soil moisture to equilibriate within each pot.

Where possible, shoot lengths were measured at the start of the experiment; shoot length at ontogeny stage one and occassionally stage two were too short to measure at this time. Shoot length, seedling mortality and predominant seedling ontogeny stage were recorded at intervals during the experiment. When 50 % or more of the seedlings of a particular ontogeny stage-soil type combination were dead and/or showed signs of wilting, the experiment was terminated for that particular combination and the live and wilted seedlings harvested. The time from the start of the run to the harvest was recorded. Buffer row seedlings were discarded. Dead seedlings were also discarded since it was uncertain at what soil moisture potential the seedlings died.

Seedling height, root length, total fresh weight and seedling condition were determined for each harvested seedling. In order to determine root length, each seedling was carefully excavated from the pot. Soil samples for soil moisture potential determination were also taken at this time for the soil depths and following the procedures outlined in the Soils section. Shoot and root dry weights were determined after drying the samples in an oven for 24 hours at 100^{o} C; samples were cooled in a desiccator before weighing. All weights were taken with the seedcoat removed.

Soil moisture content at the time of harvest was determined from the soil depth corresponding to the average final root length of the seedlings within each replication and treatment combination (seedlings harvested when 50% of the seedlings were dead and/or wilted). The corresponding soil moisture potential from the soils characteristic curve (Figure 6) was then determined. Differences between replications varied greatly, such that a mean soil moisture potential value could not be determined for each treatment combination. The greatest problem was that some soils were well below 15 bars of negative soil moisture potential; therefore, no value could be entered into the calculation of the mean. In order to obtain a mean soil moisture potential, the soil moisture content values were averaged and the soil moisture potential for this average determined. Where the soil moisture content fell below that corresponding to a soil moisture potential of -15 bars, a value of <-15 bars was recorded. The raw soil moisture content and soil moisture potential data are presented in Appendix F.

Unfortunately, fresh weight, root length and shoot and root dry weights were not determined before the start of each run. These values were determined in a supplementary experiment by sowing three pots of each soil type, ontogeny stage treatment combination and growing the seedlings under the same conditions as used during the actual experiment. For each soil type, ontogeny stage treatment combination, a weighted mean was calculated from the replication means and used in all subsequent calculations.

Initial shoot and root dry weight data could not be determined for ontogeny stages one and two for all soil types because the seedlings were too small. Only total dry weight was determined. For ontogeny

stage one, the embryo dry weight (no seed coat) was used for the initial total dry weight.

3.9.2.2 EXPERMENTAL DESIGN AND ANALYSIS OF DATA

The experiment was a split plot factorial design with wind speeds as whole plots and the soil type, ontogeny stage treatment combinations as the sub-plots. See Appendix G for the linear model and the expected mean squares table.

The treatment means and the growth increment per day since the start of the run were calculated for the shoot and root length, the fresh weight, the total shoot dry weight and, where possible, the shoot and root dry weight data. Graphs of soil moisture potential at several sampling times were drawn for each wind speed treatment.

An ANOVA was performed on the means and the growth increment data. To determine if the data met the assumptions of the ANOVA (constant variance and normality), a graphical test and the Burr-Foster Q-Test (Burr and Foster, 1972) were used to check for homoscedasticity and normality. To meet the assumptions, the data were transformed as required. Tukey's HSD method (Tukey, 1953) was used to test for differences between means. Actual means are presented in the tables, comparisons are based on the transformed means. All tests of significance were conducted at the 95 % level of confidence.

4.0 RESULTS

4.1 THE WIND TUNNEL

4.1.1 PERFORMANCE AND ENVIRONMENTAL CONDITIONS

Temperature control equipment performed well during most of the experiments. In the low wind speed ontogeny run, a heating unit relay became stuck in the open position one evening resulting in a decrease in the evening temperature to 5 °C. This was the only faulty performance of the equipment. As can be seen in Table 3, thermostats maintained the temperature at the set value with no more than a 3.4°C standard deviation.

Table 3. Mean temperature and humidity levels and mean number of sunshine hours per day for each run of the wind tunnel.

Experiment	Wind Speed	Day Temperature (°C)	Day Humidity (%)	Night Temperature (°C)	Night Humidity (%)	Sunshine Hours (hrs/day) x	Sunshine Hours (hrs/day) SD
Germination	Low*	25.6 +/-1.7	54 +/-2.3	13.4 +/-1.6	58 +/-2.3	3.6	3.1
	Mod	25.5 +/-1.5	50 +/-2.7	13.3 +/-1.7	55 +/-1.7	2.7	3.0
	High	25.6 +/-1.3	54 +/-1.9	13.3 +/-1.8	60 +/-3.0	4.5	2.4
Ontogeny	Low**	25.3 +/-1.6	56 +/-2.4	13.3 +/-1.6	60 +/-1.8	4.3	3.5
	Mod	23.7 +/-2.1	47 +/-2.4	13.1 +/-2.9	49 +/-1.8	4.6	3.8
	High	25.0 +/-2.8	48 +/-2.6	13.2 +/-3.4	51 +/-2.3	5.6	4.0

* Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr. +/- refers to standard deviation
** Calculation does not include value from the day with a relay failure.

Even though the wind tunnel was insulated it could not be run during the summer due to excessively high temperatures in the greenhouse. An attempt to do so resulted in large diurnal temperature fluctuations which were not consistent from day to day, depending on the weather.

Humidity control equipment also functioned well. Humidity levels were not consistent between wind speeds but variation within wind speeds was similar to that for temperature. The mean humidity levels decreased from the start to the end of a run. This was probabley due to a reduction in the water vapour contributed by the soil filled pots in the experiment.

Although the wind tunnel was fitted with fluorescent lights, light intensity was very dependent on the weather; unfortunately, no measurements were made at the plant surface over time to verify this statement. The mean number of sunshine hours per day, based on data recorded by Environment Canada at

the Thunder Bay weather station (Anonymous, 1985b), are also presented in Table 3 for each experimental run. There is a wide variation in sunshine hours between wind speed runs in the main germination study; however, this is probably not significant since no seed germinated. Differences are smaller between wind speed runs in the ontogony study. The maximum difference of 1 hour was not felt to affect the experimental results significantly.

There was some vibration of the working section of the wind tunnel caused by the fan and motor assembly. The amount of vibration increased with increasing wind speed. The vibration was not transferred to the pots and therefore, probably did not affect the results of the experiments.

Figure 5 (A-C) show the wind speed profile in three dimensions at 3, 10 and 20 cm above the working surface for each wind speed. For all wind speeds, the wind speed increased three centimetres above the working surface at either end of the working section relative to the centre of the working section (Figure 5A). There is also a slight increase in wind speed at the higher width and length values. The plane is slightly sloped toward the origin.

Ten centimetres above the working surface (Figure 5B) air speeds are more uniform along the length of the wind tunnel when compared to 3 cm above the working surface (Figure 5A). The increases of wind speed with increasing width are also evident, but more pronounced at the high wind speed (Figure 5C).

The wind profile varies with wind speed 20 cm above the working surface (Figure 5C). At the low wind speed there are a few peaks and valleys and a pronounced decrease in wind speed 10 cm along the width for the entire length of the wind tunnel. At the moderate wind speed there is a slight increase in wind speed at each end of the working section along with the characteristics described above for the low wind speed. At the high wind speed there are many ridges and valleys along the length of the working section. The increases at each end of the working section and the increases with increasing width are also very pronounced.

4.2 SOIL

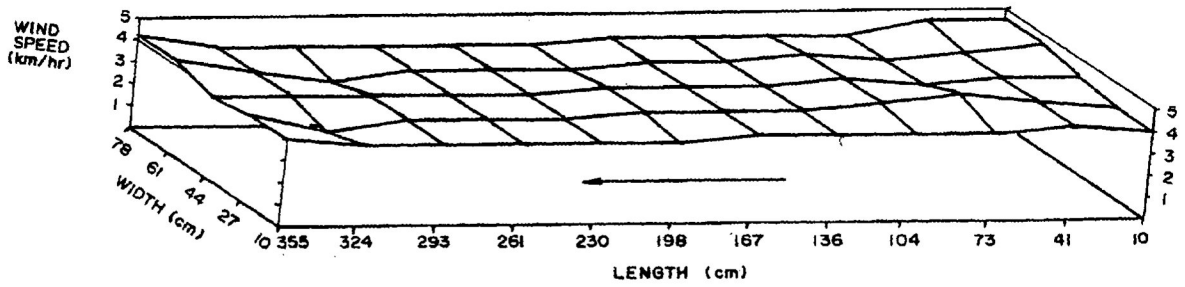
4.2.1 PHYSICAL AND CHEMICAL CHARACTERISTICS

The results of the soil texture analysis are given in Table 4; the particle size distribution for soils used in these experiments is given in Table 5. The results given in Table 5 are based on the entire soil sample and includes coarse fragments (>2.0 mm), and silt and clay (<0.05 mm). Note the high percentage of coarse fragments in the loamy sand soil. These were pebble sized stones which were not sifted out when the soil was passed through the 6.4 mm mesh screen. When the loamy sand soil was watered, these large grains littered the surface of the soil thus creating a rough textured surface.

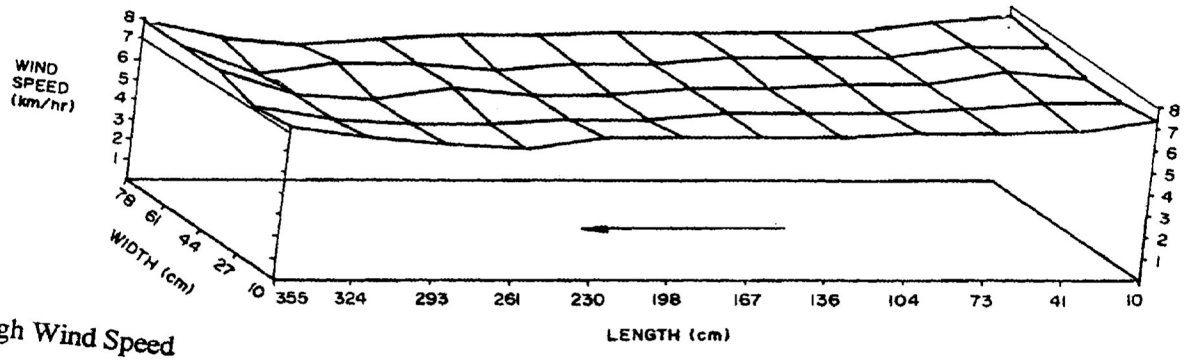
When dry, the sandy soil had a granular structure and the loamy sand and sandy loam soils had a massive structure. The latter two soil types were difficult to process, the latter of the two more than the

A. 3 cm Above The Working Surface

Low Wind Speed



Moderate Wind speed



High Wind Speed

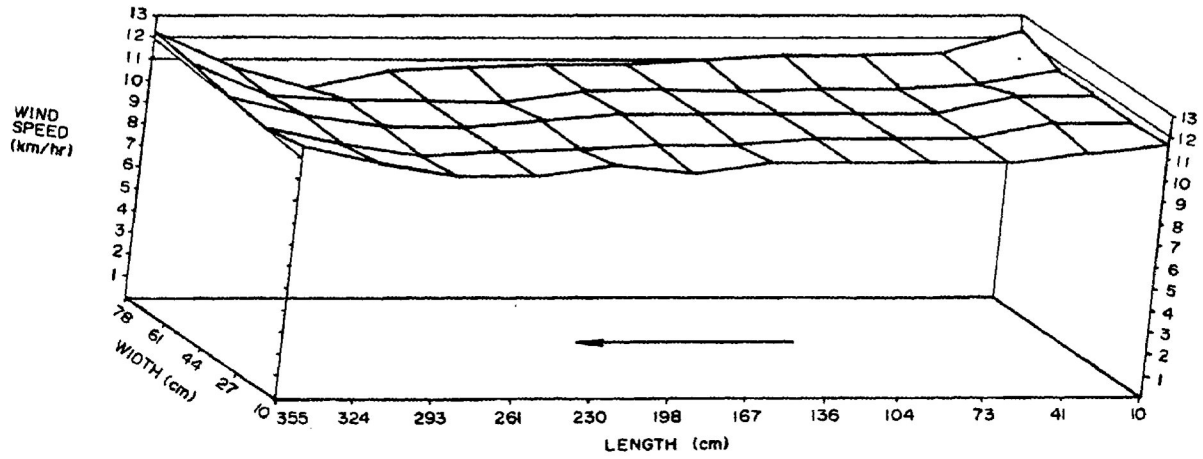
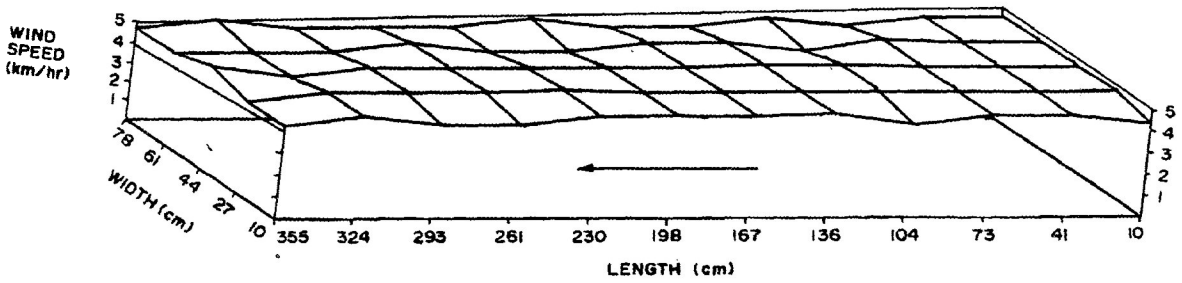


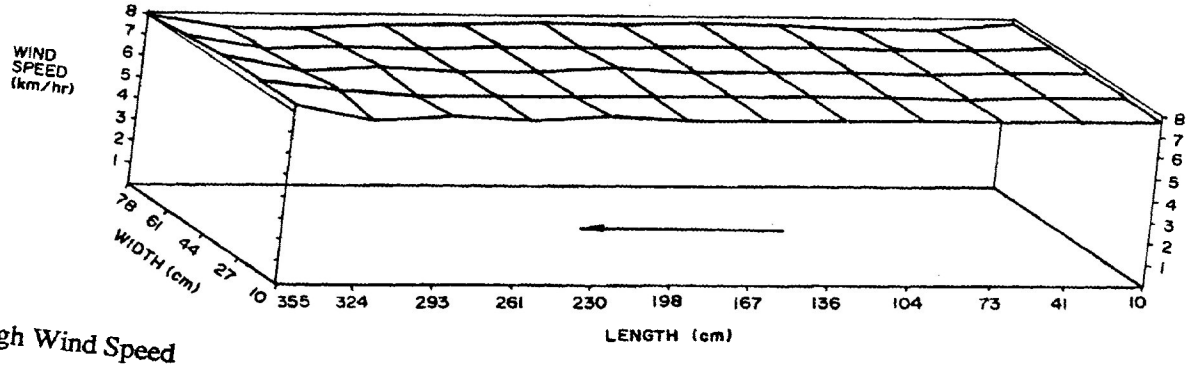
Figure 5. Wind tunnel wind speed profiles 3, 10 and 20 cm (Graph sets A, B, and C respectively) above the working surface for each wind speed. The arrow indicates wind direction. Wind Speeds: Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

B. 10 cm Above The Working Surface

Low Wind Speed



Moderate Wind speed



High Wind Speed

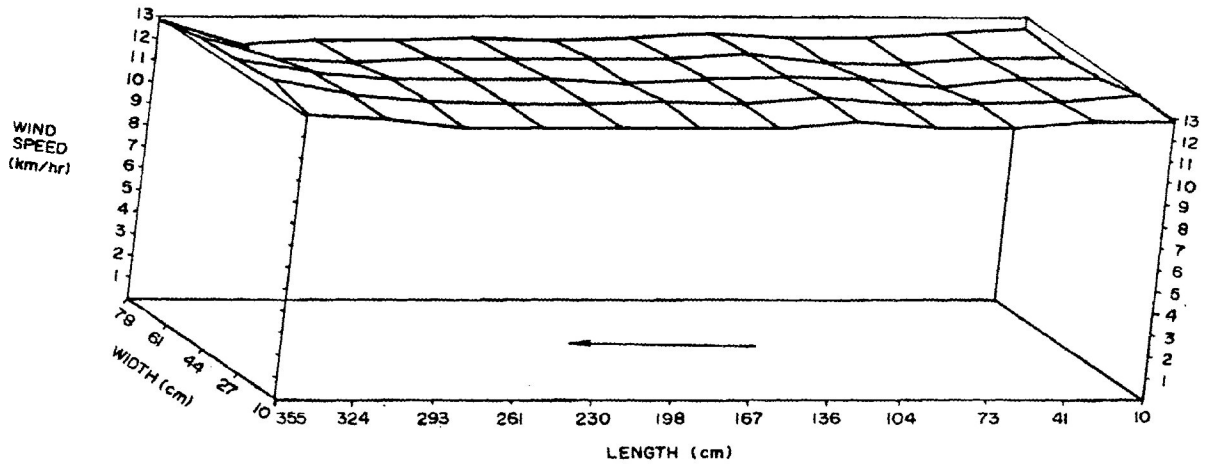
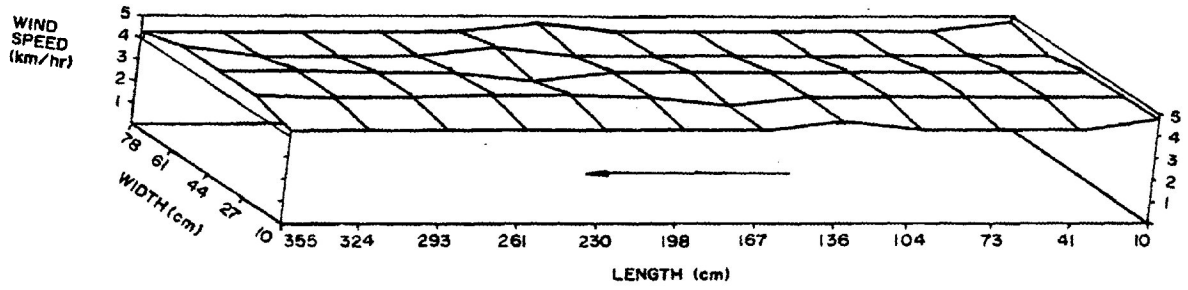


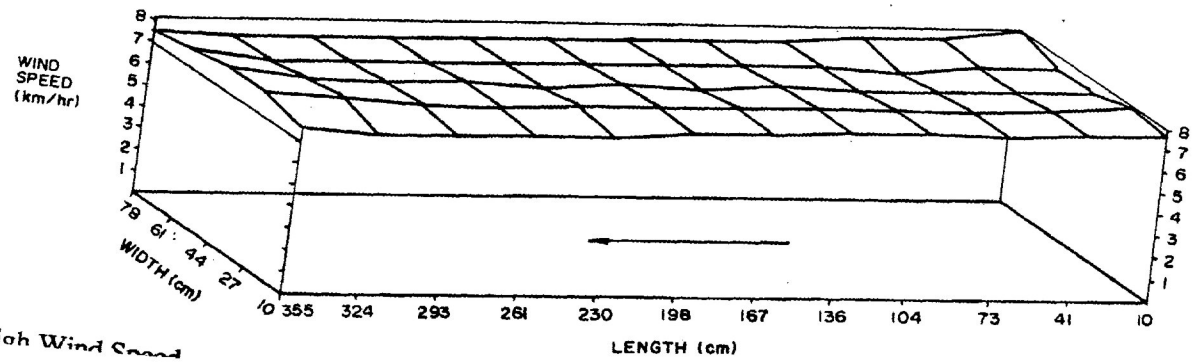
Figure 5. Continued

C. 20 cm Above The Working Surface

Low Wind Speed



Moderate Wind speed



High Wind Speed

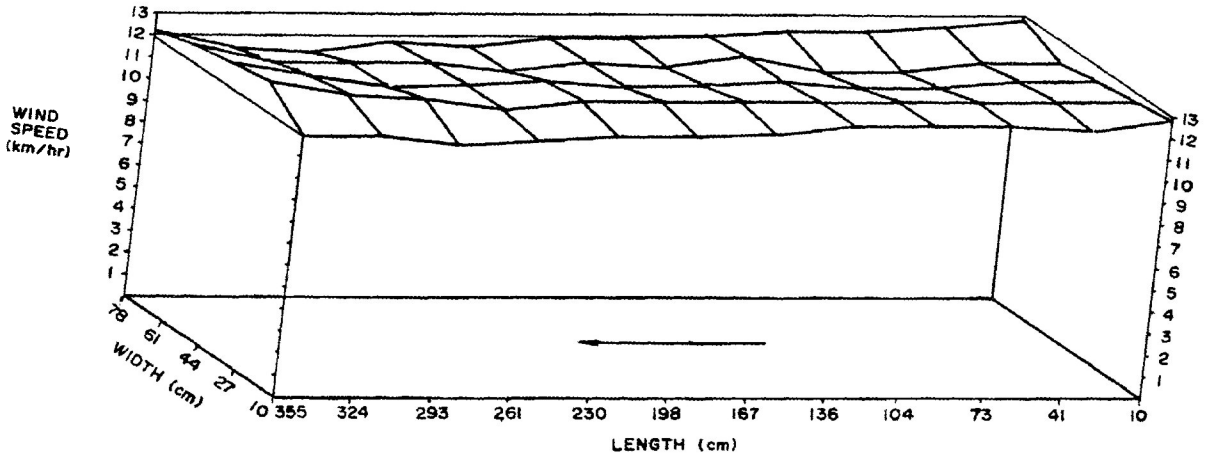


Figure 5. Continued

Table 4. Particle size distribution of the three soil types used in all experiments.

Classification	Sand (%)	Silt (%)	Clay (%)
Sand	88.0	9.1	2.9
Loamy Sand	78.0	17.0	5.0
Sandy Loam	75.6	20.8	3.6

Determined using the hydrometer method as described in Day (1965).

Table 5. Particle size distribution for soils used in all experiments.

Classification	Coarse Fragments (mm) >2.0	V. Coarse Sand 2.0-1.0	Coarse Sand 1.0-0.5	Medium Sand 0.5-0.25	Fine Sand 0.25-0.1	V. Fine Sand 0.1-0.05	Silts and Clays <0.05
				(percent)*			
Sand	1.9	5.3	16.8	41.3	27.1	5.8	1.8
Loamy Sand	15.4	15.3	20.4	23.3	13.2	4.6	7.8
Sandy Loam	1.2	2.4	8.6	23.3	16.6	18.7	8.9

*Percent values based on air dryed weight of total soil sample; this includes the coarse (>2.0 mm) and silts and clays (<0.05 mm). Texture classes based on the USDA system (see Brady, 1974).

former, because the particles were so densly packed together. The loamy sand was looser mainly due to its large pebble component.

Hydraulic conductivity of the soils, under saturated conditions was 3.72×10^{-4}, 1.26×10^{-4} and 1.08×10^{-4} cm/s for the sand, loamy sand, and sandy loam soils, respectively. As expected, the hydraulic conductivity is highest for the coarsest soil and decreases to the finest soil.

Soil surface (0-1 cm) temperature differences between soil types were less than 1°C. Soil temperatures were always below ambient when wet but increased to ambient when dry.

Results of the chemical analyses are given in Table 6. All samples were analyzed by Agri-food Laboratories as greenhouse media because tests are conducted for all macronutrients with this test procedure. The large difference in response between the start of experiments and the termination of the experiments for nitrate nitrogen, calcium and magnesium for all soils should be noted. Between the time the chemical analysis was conducted at the start of the experiment to the time the soils were analysed at the termination of the experiments Agri-food Laboratories changed their method of analysis of greenhouse media from the modified Spurway system to the saturated paste procedure. This new procedure is superior to the old system because it is faster and gives more accurate results. There is no comparison in accuracy between the two procedures (the new being superior to the old), results from the two procedures cannot be compared directly, and there is no means of converting the results of one procedure to values obtained using the other method (personal communication, Mr. Lee Battiston, Manager, Agri-food Laboratories).

The pH values dropped from before to after the experiments. This is probably a real change and not the result of the two analytical methods.

Details regarding soil bulk density and soil drying characteristics are given in the sections for the

Germination and Ontogeny experiments.

The soil moisture characteristic curve is illustrated in Figure 6. The loamy sand soil had the highest soil moisture content at any soil moisture potential followed by the sandy loam and the sandy soils, respectively. When in the wind tunnel, the surface of the sandy loam soil was visually dry before the loamy sand and sand respectively. The latter two dried within a short time of each other.

Table 6. Results of the soil chemical analysis.

Soil Texture	pH	Nitrate Nitrogen (ppm)	Phosphorus (ppm)	Potassium (ppm)	Calcium (ppm)	Magnesium (ppm)
	Prior to Start of Experiments (Using modifed Spurway method.)					
Sand	5.9	2	1	5	54	10
Loamy Sand	5.3	2	1	3	44	7
Sandy Loam	6.0	3	1	3	60	10
	After Termination of Experiments (Using saturated paste method.)					
Sand	5.5	62	1	7	54	19
Loamy Sand	4.8	44	1	4	37	17
Sandy Loam	5.3	122	1	7	116	33

All tests conducted by Agri-food Laboratories, Guelph, Ontario. Nitrogen and phosphorus expressed as totals. Potassium, magnesium and calcium expressed as exchangeable.

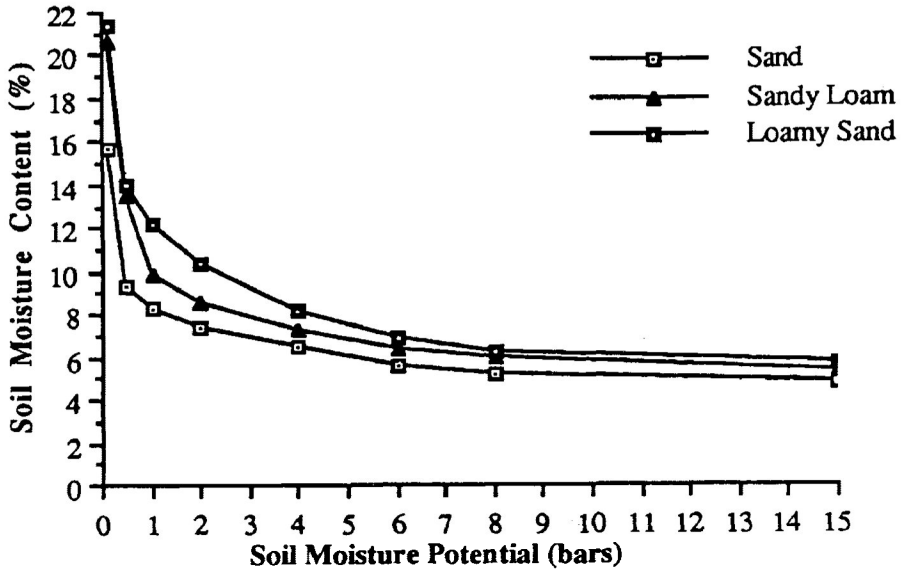


Figure 6. Soil moisture characteristic curves for the sandy, loamy sand and sandy loam soil types.

4.3 OSMOTIC PRIMING

The osmotic priming apparatus worked well except during the priming of seeds for the moderate wind speed run. During this priming run approximately 40 ml of water was lost from the priming vessel.

This was noticed 15 days into the priming run. The apparatus was checked for leaks but none were found. It was concluded that the water evaporated from the solution. Distilled water was added to the solution to bring the level of osmotic solution back to 350 ml. In all subsequent runs, the level of the solution was marked on the outside of the priming bottle with indelible marker and the solution level checked regularly.

The compressed air system kept the seeds constantly moving within the osomotic solution and appeared to keep the solution well aerated. The refrigerated cirulation unit kept the temperature of the osmotic solution at 20° C +/- 0.5° C.

Seeds germinated in Petri-dishes in a growth chamber after an osmotic priming dry run revealed no abnormal development after being transplanted to a peat vermiculite mixture.

4.4 GERMINATION STUDY

The germination study was repeated twice. This was not planned but the second germination study was included after it became apparent during the first attempt that the original study plan would have to be modified to accommodate unanticipated problems. These problems are presented in detail below. For ease of presentation of the results, the first germination study is called the preliminary germination study and the second study is the main germination study.

4.4.1 SOIL TEST RESULTS FOR THE SOIL DRYING AND GERMINATION STUDY

4.4.1.1 SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL

Figure 7 (A,B) are typical examples of soil moisture content and soil moisture potential curves for the soil drying study, preliminary germination study and ontogeny study. All further discussion is particular to Figure 7 (A,B) but in principle applies to similar graphs for the other wind speeds and soil types (See Appendix C).

Shortly after the preliminary germination study began, it became apparent that the soil was not drying as predicted in the soil drying study. A graph of the soil drying study and the preliminary germination study soil moisture content curves showed that the curves did not overlap, as expected, but ran parallel to each other especially from the 13% moisture content line (Figure 7A). This parallelism was verified when soil moisture data from the ontogeny study were also graphed and is further illustrated in the graph of soil moisture potential (Figure 7B). In the preliminary germination study, seed were sown when the soil was saturated only. No other sowing times were used because the desired soil moisture potentials could not be predicted by the curves.

The parallel nature of the soil drying study and preliminary germination study curves indicated that the soil dryed at approximately the same rate in all the studies (indicated by similar slopes) but that some

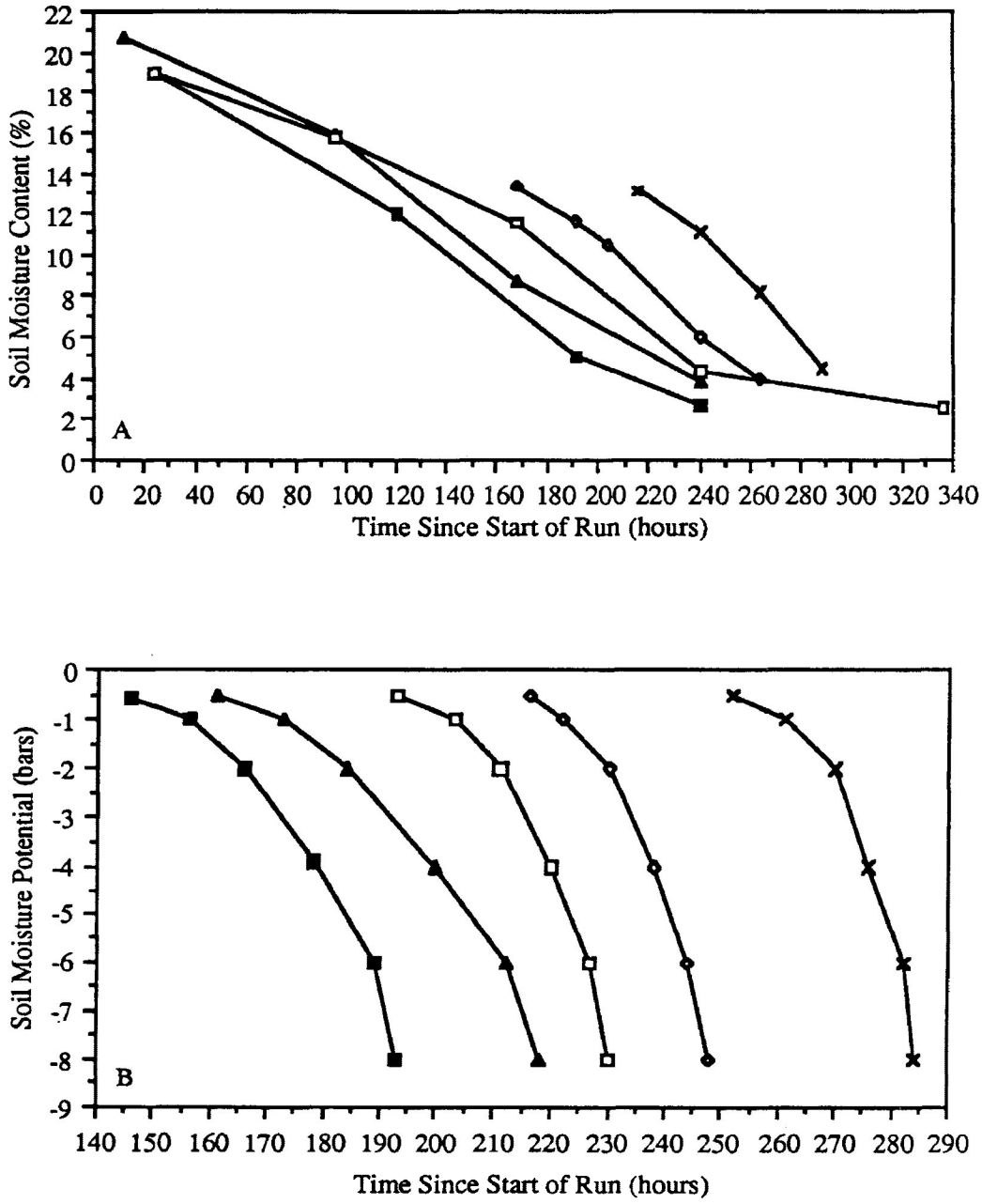


Figure 7. Soil moisture content (A) and soil moisture potential curves (B) for the soil drying study, preliminary germination study, ontogeny study and main germination study (projected drying curve, actual drying curve). Data is for the sandy soil and the low wind speed treatments of the germination and ontogeny study. Curves for the other soil type and wind speed treatments may be found in Appendix C.

physical attribute of the soil differed between runs of the same wind speed. It was hypothesized that the parallelism between the soil moisture content curves could theoretically be used to predict the soil moisture content for another germination run utilizing the soil moisture content at the start of the run as a starting point for the curve. The proper sowing times could then be interpolated from the curve. This procedure was used to predict the sowing times in the main germination study.

Figure 7 (A,B) show that the projected drying curve did not accurately predict soil drying in the main germination study for this soil type wind speed treatment combination when compared to the actual drying curve. This was also the case for the majority of the other soil type wind speed treatment combinations; consequently, the seeds in the main germination study were not sown when the soil was actually at -0.5 and -1.0 bars. As a result, most of the germination data for these two treatments could not be used. Table 7 shows the actual soil moisture potentials at which the seeds were sown in the main germination study.

Table 7. Actual soil moisture potentials at the time of sowing for the main germination study. The desired SMP's at time of sowing were 0, -0.5 and -1.0 bars.

Wind Speed	Soil Type								
	Sand			Loamy Sand			Sandy Loam		
	Soil Moisuture Potential (bars)								
Low*	0	0	0	0	-0.5	-0.8	0	-0.6	-0.7
Moderate	0	0	-0.8	0	-0.5	-0.7	0	0	-1.0
High	0	-3.6	-6.6	0	-0.6	-2.8	0	-2.5	-5.1

* Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

4.4.1.2 SOIL DRYING RATES

Figure 8 (A-C) show the change over time in soil moisture potential (0-1 and 2-4 cm depths) for each soil type and wind speed treatment combination for the main germination study. Except for the 0-1 cm depth for the low wind speed treatment, the loamy sand soil dried the fastest (i.e. had the lowest soil moisture potential) followed by the sandy loam and the sandy soil, respectively. This relationship held for both the 0-1 and the 2-4 cm depths. For the 0-1 cm depth, the sandy loam soil dried fastest followed by the loamy sand and the sandy soils respectively at the low wind speed.

4.4.1.3 BULK DENSITY

Soil bulk density data are not available for the soil drying and the preliminary germination studies. Data for the main germination study are presented in Table 8. The data show that there were minor differences in bulk density between wind speed treatments. Bulk density of the 0-9 cm depth was the highest at the moderate wind speed for all soil types. The pot refilling procedure of dropping and then

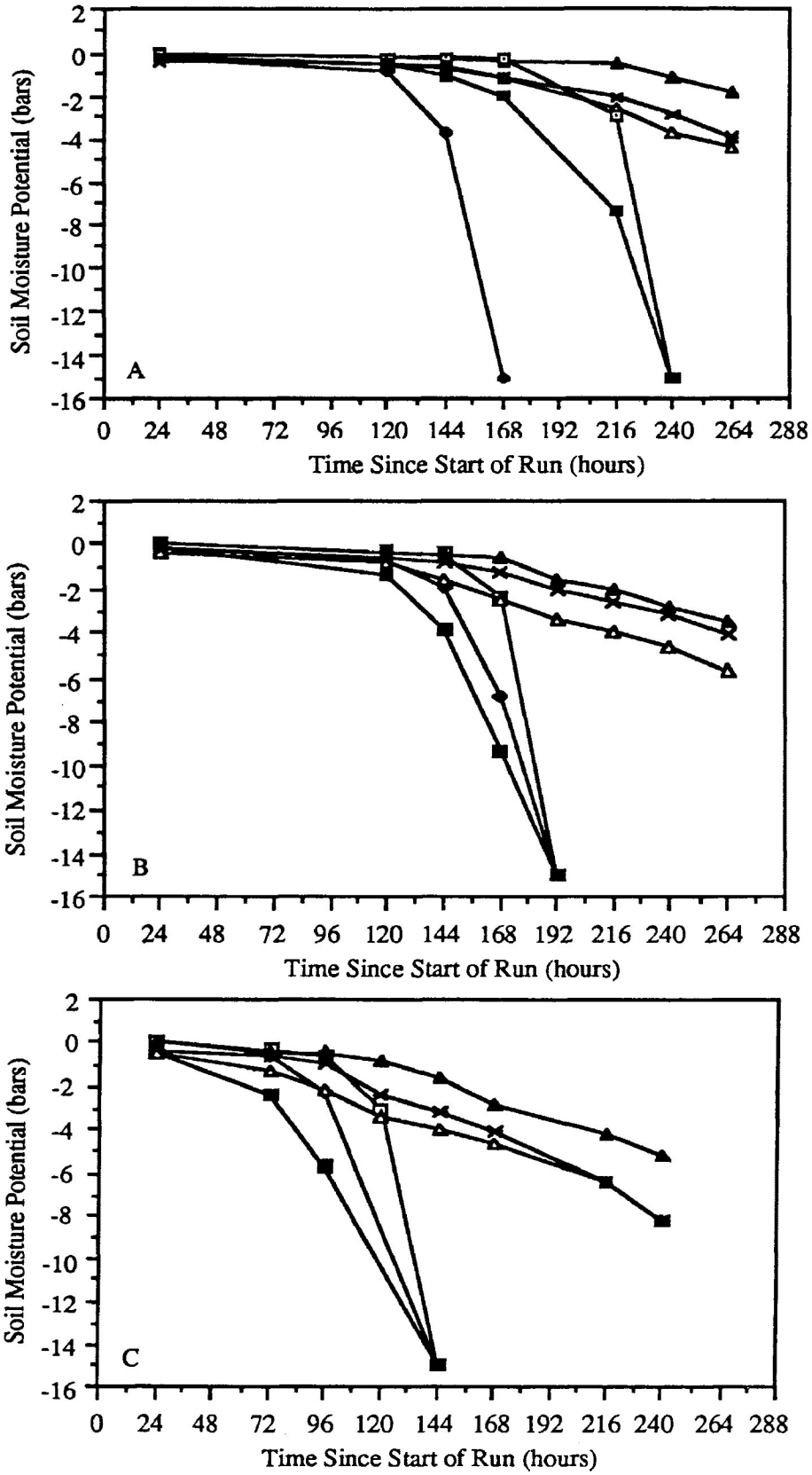


Figure 8. Soil moisture potential curves for the low (A), moderate (B) and high (C) wind speeds and for the 0-1 and 1-2 cm soil depth of the sand, loamy sand and sandy loam soils in the main germination study. 0-1 cm horizon: Sand-□-, Loamy Sand-■-, Sandy Loam-◆-. 1-2 cm horizon: Sand-▲-, Loamy Sand-△-, Sandy Loam-✱-. Wind Speeds: Low- 4.0 km/h, Moderate- 6.7 km/h km/h, High- 10.9 km/h.

weighing the pots was successful in ensuring consistant bulk densities both between and within wind speed treatments for a particular soil type. The sandy loam and the loamy sand soil types exhibited some crusting of the soil surface.

4.4.2 GERMINATION

4.4.2.1 PRELIMINARY GERMINATION STUDY

Seed did not germinate in the wind tunnel during the test. Ungerminated seeds were then removed from the soil surface and placed in petri-dishes in a growth chamber. A control lot of seed was also placed in the growth chamber. The control consisted of seed taken from cold storage and therefore not exposed to conditions in the wind tunnel. All germination results are based on the petri-dish germination data.

Graphs of the cumulative germination percent are presented in Figure 9 (A,B). Seed sown in the wind tunnel had a faster germination rate than control seeds. Forty-eight hours after being placed in the petri-dishes in the germinator, between 57 and 65 percent and 45 and 79 percent of the seed in the low and moderate wind speed runs respectively had germinated, compared to no germination for the control. The high wind speed treatment was not run. The germinative capacity of the wind tunnel sown seed is similar to that of the control indicating that wind tunnel sown seed had not lost its viability.

Table 8. Main germination study soil bulk density data, by wind speed, soil type, and soil depth (values are the mean of three pots with two samples per depth).

Soil Type	Wind Speed	Depth (cm) 0-9		9-15	
		BD*	CV**	BD	CV
Sand	Low***	1.4	1.5	1.4	0.2
	Mod	1.4	0.8	1.4	0.4
	High	1.4	0.8	1.4	1.4
Loamy Sand	Low	1.4	0.9	1.4	0.2
	Mod	1.4	1.6	1.4	1.6
	High	1.4	1.2	1.4	0.8
Sandy Loam	Low	1.3	0.8	1.4	0.6
	Mod	1.4	0.8	1.4	0.7
	High	1.3	0.6	1.4	1.2

* Bulk Density (gm/cm^3) ** Coefficient of Variation (%)
*** Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

The relationship between the germination curves of the wind tunnel sown seed and the control seed indicates that the seed of the former imbibed a sufficient amount of water to begin the germination process but not enough to complete it. This is evident by the rapid germination compared to the control after the seed were rehydrated in the growth chamber test. This is similar to the effect of osmotically priming seed

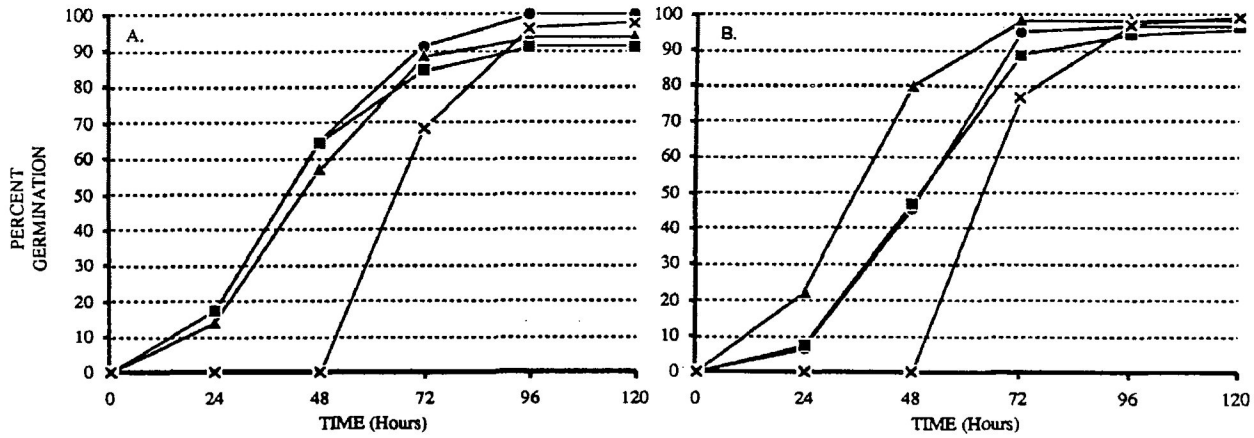


Figure 9. Cumulative germination percent for the growth chamber germination test of the preliminary germination study. A) Low wind speed wind tunnel run (4.0 km/h). B) Moderate wind speed wind tunnel run (6.7 km/h). • Sandy Soil, ■ Loamy Sand, ▲ Sandy Loam, × Control.

in an osmotic solution.

It was hypothesized that if the seed in another run of the germination test were osmotically primed before being placed in the wind tunnel, they then would begin the germination process from the point that the wind tunnel sown seed in the previous study left off and would therefore germinate in the wind tunnel. To test this hypothesis, the experiments were modified to include treated (osmotically primed) and untreated seed.

To accomodate this modification, the experimental design was modified. Fewer soil moisture potentials were selected as sowing times since more pots would be needed to accomodate the seed treatment. Additionally, since the seed failed to germinate when the soil was saturated, they would probably not germinate at any of the extreme soil moisture potentials. To test germination at these soil moisture potentials would therefore be futile.

4.4.2.2 MAIN GERMINATION STUDY

As in the preliminary germination study, seed did not germinate in the wind tunnel. All germination results are based on the growth chamber Petri-dish germination tests. Seed were transfered from the pots in the wind tunnel to Petri dishes and the germination monitored. A control lot of seed was also placed in Petri-dishes in the growth chamber. The control consisted of primed and unprimed seed taken from cold storage and therefore not subjected to the treatments in the wind tunnel. After 168 hours in the growth chamber, ungerminated seed were dissected to determine if they were sound. A majority of the ungerminated seed were sound. The germination percent calculations are based on the total number of sound seed (germinated and sound ungerminated). Figure 10 (A-F) show the cumulative germination

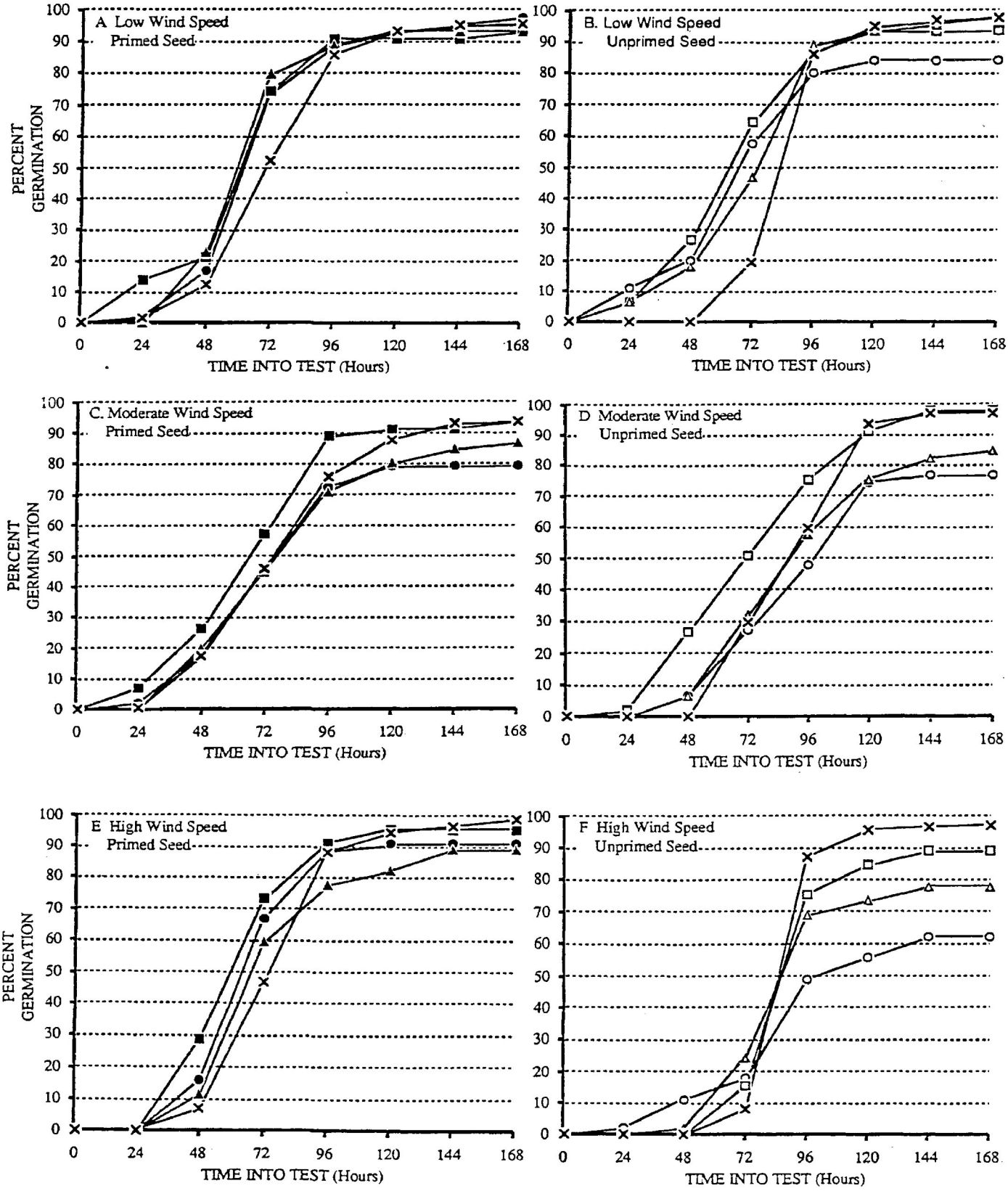


Figure 10. Graphs of the cumulative germination percent for the wind tunnel sown seed versus the control seed by seed treatment, soil type and wind speed. Sand Primed -●- , Sand Unprimed -○- , Loamy Sand Primed -■-, Loamy Sand Unprimed -□- , Sandy Loam Primed -▲- , Sandy Loam Unprimed -△-, Control -×-.

percent by wind speed, soil type and seed treatment. Tables of the data may be found in Appendix D. The ANOVA tables and lists of required transformations may be found in Appendix B.

There were significant ($p>0.05$) differences (Appendix B-I) in germination percent between the primed and unprimed wind tunnel sown seed 48, 72 and 96 hours after the start of the germination test. After these times there were no significant differences. Analysis of variance of the results for each wind speed revealed that there was a significant difference in germination rate between seed treatments for the high wind speed treatment at all recording times (Appendix B-II). Numerical differences between the seed treatments varied with wind speed and soil type treatment, the least difference occuring at the low wind speed treatment and the greatest difference at the high wind speed treatment. The effects of wind speed and soil type on primed versus unprimed seed is presented in more detail below.

The control seed (primed and unprimed seed taken from cold storage) were used as a reference in order to compare the germination of seed receiving the wind speed and soil type treatments to seeds not receiving these treatments. For the primed seed, the germination percent of the wind tunnel sown seed was greater than or equal to that of the control primed seed for all wind speed and soil type treatments. This relationship held up to 72 hours after the start of the germination tests. After 72 hours, germination percent for the sandy and sandy loam soil treatments fell slightly below that of the control, mainly for the moderate and high wind speed treatments. The germination percent was never significantly less than that of the control at any wind speed (Appendix E). The higher germination percent at times up to 72 hours after the start of the growth chamber test indicates that the seed did absorb some additional water. More rapid germination is indicative of some additional water absorption. Wind speed and soil type had little effect on the primed seed.

At the low wind speed germination of the unprimed seed was similar to that of the primed seed. Germination percent for the unprimed wind tunnel sown seed was higher than that of the control up to 72 hours after the start of the growth chamber germination tests after which they were equal to or slighly less than the control.

As wind speed increased the germination percent of the unprimed seed was affected more, the magnitude of the affect varying with soil type. At the moderate wind speed germination of seed sown on the sand and the sandy loam soils approached that of the control up to 72 hours after the start of the test after which it fell below that of the control. The differences were not significant. Germination of seed sown on the loamy sand was similar to that at the low wind speed; the increase in wind speed had no affect on germination. At the high wind speed germination of unprimed seed sown on all soil types was similar to that of the control up to 72 hours and below that of the control after 72 hours. The germination percent of seed sown on the sandy soil was significantly different from that of the control at times 96 and 168. All other differences between the wind tunnel sown seed and the control were insignificant.

It is to be noted that the germination of unprimed seed decreased with each increase in wind speed, the magnitude of the decrease varying with soil type. This is especially evident for the sandy soil type.

The combined effect of wind speed and soil type, although not statistically signficant, is affecting the germination of the unprimed seed. Germination of primed seed was not similarily affected.

The wind tunnel could accomodate only one wind speed treatment at a time. As a result, one lot of seed (seedlot) was osmotically primed in advance of each wind tunnel run. The curves of the control treatment show that there was little numerical difference between lots of seed prepared for each wind speed run. Due to the nature of the experimental design, there was no statisitical test between seedlots.

A comparison of primed versus unprimed control seed treatments showed that the germination of the primed seed was significantly higher than the unprimed seed up to 72 hours after the start of the germination test (Appendix B-III). After this time germination percents were similar.

4.5 ONTOGENY STUDY

4.5.1 SOILS

The graphs of soil moisture potential versus time for each wind speed (Figure 11 (A-C)) show that, with a few exceptions, the loamy sand soil dried the fastest (*viz.* reached low soil moisture potentials the quickest), followed by the sandy loam and sandy soil, respectively. This relationship does not hold for the shallow depths 192 and 408 hours after the start of the wind tunnel run for the moderate wind speed nor for the shallow depths at 192 hours and for all soil depths at 408 hours at the high wind speed. As wind speed increased, the soil at deeper depths dried faster. The rate of drying was fastest for the loamy sand soil and slowest for the sandy soil.

Soil bulk density is given in Table 9 for the three wind speeds, by soil type, for the top and the bottom of the pot (0-9 and 9-15 cm from the soil surface, respectively). Differences within soil types within wind speeds were minor.

All three soil types had crusting of the surface; crusting was less severe for the sandy soil and most severe for the sandy loam soil. In the wind tunnel, the surface of the sandy loam appeared to dry before that of the loamy sand and sandy soils, respectively. The latter two appeared dry within a short time of each other. When dry, the structure of the sandy soil was loose and granular as opposed to that of the loamy sand and sandy loam which was hard and crusted.

4.5.2 INITIAL GERMINANT CHARACTERISTICS

Table 10 shows the results of the supplementary tests to determine initial germinant characteristics. These values were used as the initial values in all increment calculations. The same values were used for each wind speed test. Shoot and root dry weight values for ontogeny stages one and two could not be determined because the seedlings were too small to measure these components separately.

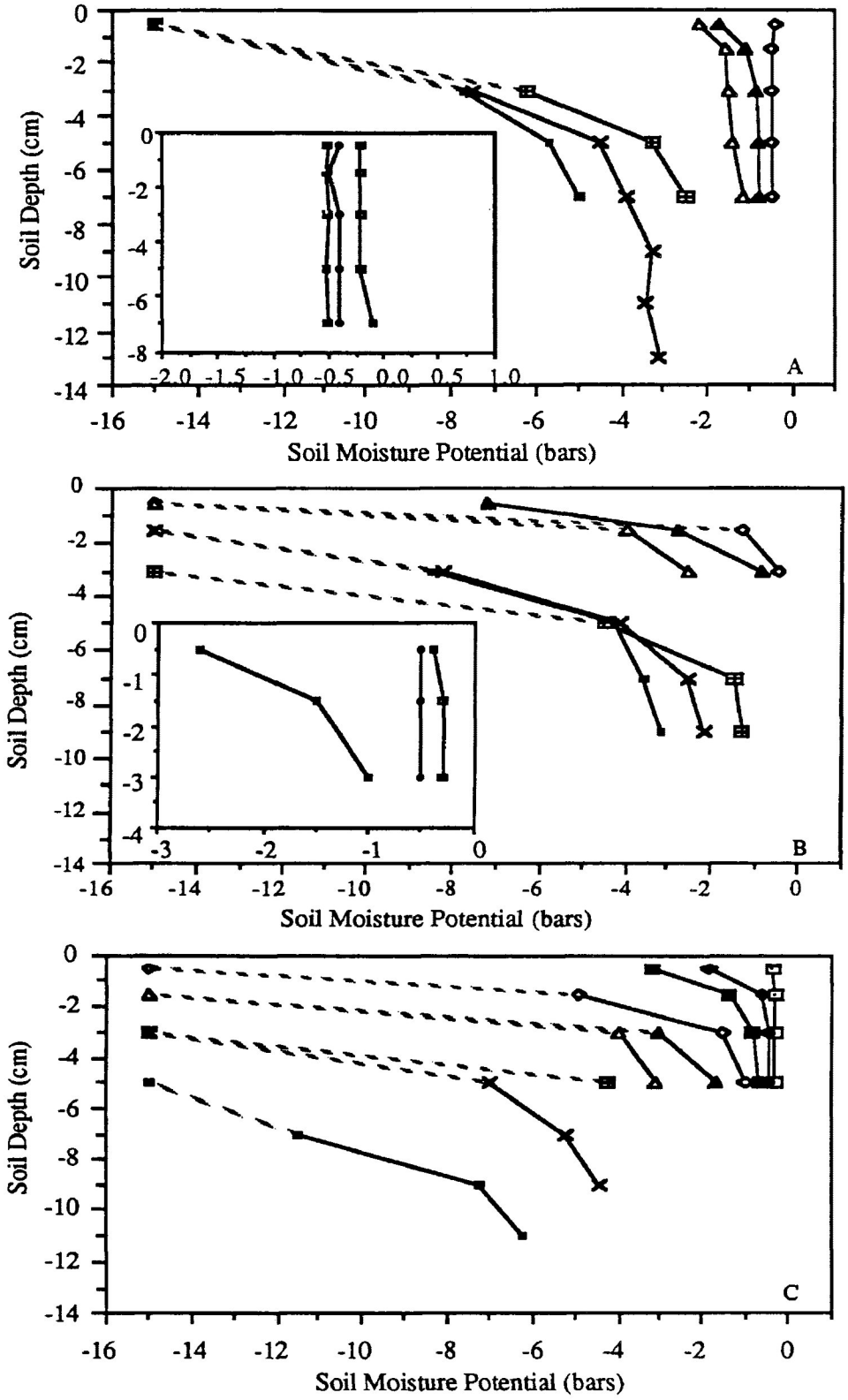


Figure 11. Soil moisture potential through the soil profile for the low (A), moderate (B) and high (C) wind speed and by soil type treatment at several sampling times for the ontogeny study. Soil types and sampling times: Sand t=120, Loamy Sand t=120, Sandy Loam t=120, Sand t=192, Loamy Sand t=192, Sandy Loam t=192, Sand t=408, Sandy Loam t=408, Loamy Sand t=408. For some horizons the soil moisture potential fell below -15 bars and could not be determined accurately. These values are represented by ~~~~~~~~~.
Wind speeds: Low- 4.0 km/h, Moderate- 6.7 km/h, High- 10.9 km/h.

Table 9. Soil bulk densities by wind speed and soil type treatment, measured at time of harvest (Time when 50% or more of the germinants were dead and/or wilted).

Soil Type	Wind Speed	Soil Depths (cm) 0-9		9-15	
		BD*	CV**	BD	CV
Sandy	Low***	1.5	-	1.5	-
	Moderate	1.3	4.3	1.4	1.1
	High	1.5	0.4	1.4	1.6
Loamy	Low	1.4	2.9	1.4	2.3
Sand	Moderate	1.2	2.4	1.4	0.2
	High	1.4	1.4	1.4	3.5
Sandy	Low	1.4	2.2	1.5	2.8
Loam	Moderate	1.3	1.0	1.4	9.0
	High	1.4	1.7	1.4	1.0

* Bulk Density (gm/cm^3) ** Coefficient of Variation (%)
*** Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

Table 10. Initial germinant characteristics by ontogeny stage and soil type.

Ontogeny Stage	Soil* Type	Total Seedling Dry Wt. (mg)	Root Length (mm)	Shoot Dry Wt. (mg)	Root Dry Wt. (mg)
	S	2.1	0.0	na	na
1	LS	2.1	0.0	na	na
	SL	2.1	0.0	na	na
	S	2.3	4.8	na	na
2	LS	2.1	5.4	na	na
	SL	2.3	3.2	na	na
	S	2.2	14.9	1.8	0.4
3	LS	2.1	13.4	1.7	0.4
	SL	1.9	8.5	1.7	0.2
	S	2.4	24.2	1.9	0.5
4	LS	2.0	20.7	1.6	0.4
	SL	2.1	12.0	1.7	0.4
	S	2.7	25.2	2.1	0.6
5	LS	2.8	28.4	2.2	0.6
	SL	2.5	16.4	2.0	0.5

Initial height data are not presented but were recorded by replication, soil type, ontogeny stage and wind speed at the start of each run. Summarys of these data will be presented when and where necessary. The seedcoat was removed in all cases.
*S- Sand LS- Loamy Sand SL- Sandy Loam.

4.5.3 FINAL RESULTS

For the sandy soil type, time to harvest within an ontogeny stage changes little as wind speed increases (Table 11). Values for the loamy sand and sandy loam soils change little from the low to moderate wind speed then decrease from the moderate to high wind speed. Values increase from ontogeny stage one to five for all soil type and wind speed treatments.

At the low wind speed, there was little difference in survival time between soil types. At the high wind speed the difference was greater. At the high wind speed, germinants survived longer for the sandy soil treatment than for the loamy sand and sandy loam soil treatments.

At the low wind speed, seedlings at all ontogeny stages grown in the sandy soil and all but ontogeny stage one of the loamy sand soil did not begin to die until the soil was below -15 bars. This contrasts with the sandy loam soil in which the germinants at all ontogeny stages began to die at or above (smaller negative) -15 bars.

Table 11. Time to harvest (time when 50% or the seedlings are dead and/or wilted) and soil moisture potential at root tip depth at time of harvest for each soil type, ontogony stage, wind speed treatment combination.

Wind Speed	Soil* Type	Ontogeny Stage 1	2	3	4	5
		Time to Harvest (days)/Moisture Potential at Root Tip (bars)				
	S	20/<-15.0	23/<-15.0	29/<-15.0	31/<-15.0	32/<-15.0
Low	LS	18/ -8.2	25/<-15.0	27/<-15.0	30/<-15.0	33/<-15.0
	SL	17/ -8.0	19/ -15.0	22/ -14.7	26/ -15.0	28/ -14.8
	S	15/ -3.2	21/ -4.4	29/ -6.6	31/ -6.2	37/<-15.0
Moderate	LS	17/ -6.2	22/ -6.2	28/ -6.7	31/ -6.7	36/ -12.0
	SL	16/ -8.5	22/ -10.2	27/ -15.0	30/<-15.0	36/<-15.0
	S	18/ -4.2	25/ -5.9	29/ -15.0	31/<-15.0	32/<-15.0
High	LS	0/ na	14/ -8.2	20/<-15.0	21/ -9.3	23/ -8.7
	SL	0/ na	13/ -11.3	15/ -6.2	16/ -13.0	17/ -8.0

*S- Sand LS- Loamy Sand SL- Sandy Loam
**Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

At the high wind speed, except for ontogeny stages one and two, germinants grown on the sandy soil type died at or below -15 bars. Except for ontogeny stage three, this is similar to the performance at the low wind speed. Germinants grown in the sandy loam and loamy sand soil types at the high wind speed generally died at soil moisture potentials above (smaller negative) those at the low wind speed.

The total, shoot and root dry weight increment and value data may be found in Table 12 and the shoot and root length increment and value data may be found in Table 13.

For ontogeny stages one and two, germinants grown on the sand were generally affected less by increasing wind speed than those grown on the sandy loam and loamy sand soil types. There was no

Table 12. Total, shoot and root dry weight increment (mg/day) and values (mg) at time of harvest (Time when 50% or more of the germinants were dead and/or wilted) by wind speed, soil type and ontogeny stage.

Wind Speed	Soil* Type	Ontogeny Stage 1	2	3	4	5
		Total Dry Weight Increment (mg/day)/Total Dry Weight Value (mg)				
	S	0.06/ 3.28^{b-f}	0.10/ 4.55^{d-h}	0.15/ 6.62^{h-m}	0.16/ 7.58^{j-o}	0.23/10.08^{m-r}
Low**	LS	0.03/ 2.60^{bc}	0.11/ 4.85^{f-i}	0.13/ 5.60^{g-l}	0.19/ 7.70^{k-o}	0.24/10.65^{n-s}
	SL	0.02/ 2.50^{bcd}	0.06/ 3.40^{b-g}	0.16/ 5.45^{g-k}	0.18/ 6.65^{h-m}	0.20/ 8.17^{k-q}
	S	0.05/ 2.85^{b-e}	0.12/ 4.73^{e-j}	0.25/ 9.42^{m-r}	0.31/12.10^{p-s}	0.35/15.52^{s}
Mod	LS	0.02/ 2.45^{b}	0.08/ 3.88^{b-g}	0.21/ 7.95^{k-p}	0.27/10.40^{m-s}	0.30/13.50^{rs}
	SL	0.02/ 2.50^{b}	0.08/ 3.95^{b-g}	0.21/ 7.58^{i-o}	0.31/11.38^{o-s}	0.38/16.20^{s}
	S	0.05/ 2.92^{b-e}	0.12/ 5.18^{f-k}	0.24/ 9.02^{m-r}	0.32/12.55^{qrs}	0.39/15.15^{s}
High	LS	0.00/ 0.00^{a}	0.03/ 2.50^{b}	0.14/ 4.88^{f-j}	0.27/ 7.72^{k-o}	0.37/11.38^{o-s}
	SL	0.00/ 0.00^{a}	0.01/ 2.33^{b}	0.17/ 4.40^{c-h}	0.31/ 7.10^{i-n}	0.38/ 8.97^{l-r}
		Shoot Dry Weight Increment (mg/day)/Shoot Dry Weight Value (mg)				
	S	- / 2.35^{b-e}	- / 3.28^{efg}	0.10/ 4.68^{g-k}	0.12/ 5.58^{i-n}	0.16/ 7.12^{l-q}
Low	LS	- / 1.82^{b-d}	- / 3.40^{e-g}	0.09/ 4.10^{f-j}	0.13/ 5.60^{i-n}	0.16/ 7.42^{m-r}
	SL	- / 1.75^{bcd}	- / 2.40^{b-e}	0.11/ 4.10^{f-j}	0.12/ 4.80^{g-l}	0.15/ 6.10^{j-p}
	S	- / 1.88^{bcd}	- / 3.60^{e-i}	0.17/ 6.72^{k-q}	0.20/ 8.25^{n-s}	0.23/10.62^{rs}
Mod	LS	- / 1.60^{b}	- / 2.72^{b-f}	0.14/ 5.75^{j-o}	0.19/ 7.43^{m-s}	0.20/ 9.50^{qrs}
	SL	- / 1.72^{bc}	- / 2.78^{c-f}	0.14/ 5.62^{i-n}	0.22/ 8.38^{o-s}	0.26/11.40^{s}
	S	- / 1.98^{bcd}	- / 3.65^{e-h}	0.16/ 6.45^{k-p}	0.22/ 8.70^{p-s}	0.26/10.45^{rs}
High	LS	- / 0.00^{a}	- / 1.78^{bc}	0.10/ 3.60^{e-h}	0.19/ 5.62^{i-n}	0.26/ 8.28^{o-s}
	SL	- / 0.00^{a}	- / 1.67^{bc}	0.09/ 3.10^{d-g}	0.23/ 5.32^{h-m}	0.27/ 6.57^{k-q}
		Root Dry Weight Increment (mg/day)/Root Dry Weight Value (mg)				
	S	- / 0.88^{o-u}	- / 1.28^{j-q}	0.05/ 1.72^{f-m}	0.05/ 1.92^{e-m}	0.06/ 2.55^{a-h}
Low	LS	- / 0.78^{r-u}	- / 1.42^{i-o}	0.04/ 1.53^{g-n}	0.06/ 2.10^{c-j}	0.07/ 2.95^{a-f}
	SL	- / 0.65^{tu}	- / 1.00^{n-u}	0.05/ 1.38^{i-p}	0.05/ 1.80^{f-m}	0.06/ 2.10^{d-j}
	S	- / 0.95^{n-u}	- / 1.20^{l-u}	0.08/ 2.70^{a-g}	0.11/ 3.82^{a-d}	0.12/ 4.95^{a}
Mod	LS	- / 0.85^{p-u}	- / 1.18^{m-u}	0.06/ 2.15^{b-j}	0.08/ 2.97^{a-g}	0.10/ 4.05^{abc}
	SL	- / 0.78^{q-u}	- / 1.15^{k-u}	0.07/ 1.98^{e-l}	0.09/ 3.02^{a-f}	0.11/ 4.80^{ab}
	S	- / 0.95^{n-u}	- / 1.50^{h-n}	0.08/ 2.60^{a-h}	0.11/ 3.80^{a-d}	0.13/ 4.65^{a}
High	LS	- / 0.00^{v}	- / 0.72^{stu}	0.04/ 1.30^{j-p}	0.08/ 2.12^{d-j}	0.11/ 3.22^{a-e}
	SL	- / 0.00^{v}	- / 0.67^{u}	0.07/ 1.30^{i-t}	0.09/ 1.85^{e-m}	0.12/ 2.37^{a-i}

No data are available for ontogeny stages one and two. There is no significant difference between the means for any of the increment data. For the balance of the data, means with the same letter within a response variable are not significantly different at p=0.05. * S- Sand LS- Loamy Sand SL- Sandy Loam.** Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.

difficulty with the establishment and growth of ontogeny stage one and two germinants on the sandy soil at the moderate and high wind speed. For the loamy sand and sandy loam soil treatments, establishment and growth were poor at the moderate wind speed. At the high wind speed, ontogeny stage one germinants died so soon after radicle emergence that no response could be determined. Ontogeny stage two germinants

survived but grew very little even though the radicle was already in the soil when the experiments began.

Table 13. Shoot length and root length increments and values at time of harvest (Time when 50% or more of the germinants were dead and/or wilted) and shoot lengths at start of experiments.

Wind Speed	Soil* Type	Ontogeny Stage 1	2	3	4	5
		Final Shoot Length Increment/Root Length Increment (mm/day)				
Low**	S	1.16^{abc}/1.71^{a-d}	0.90^{cd} /1.59^{ab}	0.41^{ef} /1.51^{a}	0.07^{k-q} /1.41	0.03^{pq} /1.61^{ab}
	LS	1.13^{abc}/1.78^{a-d}	0.86^{d} /1.94^{a-g}	0.40^{ef} /1.63^{a-d}	0.06^{k-q} /1.64^{abc}	0.03^{pq} /1.61^{ab}
	SL	1.28^{a} /1.90^{a-i}	1.02^{a-d} /1.73^{a-e}	0.50^{e} /1.90^{a-g}	0.11^{j-o} /1.88^{a-f}	0.02^{pq} /1.87^{a-e}
Mod	S	1.11^{a-d} /2.90^{h-m}	1.08^{a-d} /3.10^{i-m}	0.27^{ghi}/3.09^{j-m}	0.13^{jk} /2.88^{h-m}	0.07^{k-q} /2.64^{e-m}
	LS	0.94^{a-d} /2.26^{a-k}	0.91^{bcd}/2.54^{d-l}	0.20^{hij} /2.29^{b-k}	0.14^{jk} /2.36^{b-l}	0.08^{k-p} /2.06^{a-i}
	SL	1.15^{abc}/2.16^{a-j}	1.03^{a-d}/2.02^{a-h}	0.33^{fg} /2.28^{a-k}	0.12^{jkl} /2.63^{e-m}	0.03^{opq}/2.85^{g-m}
High	S	1.15^{abc}/3.31^{lm}	0.86^{d} /3.23^{klm}	0.19^{ij} /3.32^{lm}	0.05^{l-q} /3.37^{lm}	0.04^{l-q} /3.65^{m}
	LS	0.00^{q} /0.00^{o}	1.18^{ab}/1.68^{abc}	0.29^{fgh}/1.78^{a-d}	0.04^{m-q}/2.45^{c-l}	0.05^{l-q} /2.98^{i-m}
	SL	0.00^{q} /0.00^{o}	1.24^{a} /2.08^{a-j}	0.56^{e} /2.85^{f-n}	0.04^{n-q} /3.74^{m}	0.02^{pq} /3.60^{lm}
		Shoot Length Values at Start of Experiments (mm)***				
Low	S	0.00^{a}	3.31^{b}	15.01^{cd}	24.39^{n}	23.60^{lmn}
	LS	0.00^{a}	2.62^{b}	15.00^{cd}	24.28^{mn}	23.22^{lmn}
	SL	0.00^{a}	2.06^{b}	15.43^{cd}	21.22^{i-n}	23.40^{lmn}
Mod	S	0.00^{a}	0.00^{a}	16.72^{c-f}	19.31^{f-k}	21.67^{j-n}
	LS	0.00^{a}	0.00^{a}	18.50^{e-i}	18.90^{f-k}	21.18^{i-n}
	SL	0.00^{a}	0.00^{a}	17.81^{d-h}	21.80^{j-n}	23.73^{l-n}
High	S	0.00^{a}	0.00^{a}	16.96^{c-g}	20.66^{h-l}	22.41^{k-n}
	LS	0.00^{a}	0.00^{a}	15.75^{c-e}	19.06^{f-j}	19.80^{g-k}
	SL	0.00^{a}	0.00^{a}	14.04^{c}	20.33^{h-l}	20.72^{h-m}
		Final Shoot Length Values/Root Length Values (mm)				
Low	S	23.2^{h-o}/ 34.1^{abc}	24.0^{i-o} / 41.4^{a-e}	26.9^{o} / 58.8^{e-k}	26.4^{no} / 68.0^{g-m}	24.6^{k-o}/ 76.8^{k-p}
	LS	20.4^{c-j} / 32.1^{ab}	24.0^{i-o} / 53.9^{d-j}	25.8^{mno}/ 57.5^{e-k}	26.4^{no} / 69.9^{j-o}	24.3^{j-o} / 81.7^{l-r}
	SL	21.8^{e-n}/ 32.2^{abc}	21.5^{e-m} / 36.1^{a-d}	26.4^{no} / 50.2^{c-i}	24.2^{j-o} / 61.0^{f-l}	24.0^{i-o} / 68.8^{g-n}
Mod	S	16.6^{bcd}/ 43.5^{a-f}	22.6^{g-o} / 69.9^{g-o}	24.5^{k-o} /104.5^{r-u}	23.5^{h-o}/113.6^{s-u}	24.2^{j-o} /123.0^{tuv}
	LS	16.0^{b} / 38.4^{a-d}	20.0^{b-i} / 61.3^{f-l}	24.0^{j-o} / 77.4^{k-p}	23.2^{h-o}/ 93.8^{o-s}	24.0^{i-o} /102.8^{q-u}
	SL	18.4^{b-g}/ 34.6^{abc}	22.6^{f-n} / 47.8^{b-f}	26.7^{o} / 70.0^{j-o}	25.3^{l-o} / 91.0^{n-s}	24.9^{k-o}/119.0^{s-v}
High	S	20.7^{d-k}/ 59.6^{f-k}	21.5^{e-m}/ 85.6^{m-r}	22.4^{e-n} /111.3^{stu}	22.2^{e-m}/128.6^{uv}	23.8^{h-o}/142.0^{v}
	LS	0.0^{a} / 0.0^{w}	16.5^{bc} / 29.0^{a}	21.6^{e-m} / 48.9^{c-i}	19.9^{b-h} / 72.1^{j-o}	21.0^{e-k}/ 97.0^{p-t}
	SL	0.0^{a} / 0.0^{w}	16.1^{bc} / 30.2^{ab}	22.5^{e-o} / 51.2^{c-j}	21.0^{e-k} / 71.9^{j-o}	21.1^{e-l} / 77.5^{k-q}

* S- Sand LS- Loamy Sand SL- Sandy Loam. For a particular response variable, means with the same letter are not significantly different at p= 0.05. ** Low- 4.0 km/hr, Moderate- 6.7 km/hr, High- 10.9 km/hr.
*** Initial root length values may be found in Table 10.

For the ontogeny stage one germinants, total and shoot dry weight values for the sandy soil treatment decreased from the low to moderate wind speed then changed little from the moderate to high wind speed whereas those for the sandy loam and loamy sand soil types decreased or changed little from

the low to the moderate wind speed. Germinants failed to establish at the high wind speed. There was no significant difference in total dry weight or shoot length increment with increasing wind speed for all the soil types. Shoot length values for the sandy soil type decreased from the low to moderate wind speed then increased from the moderate to high wind speed whereas for the finer soil types it decreased with increasing wind speed. These results contrast with those of the root data. Root length increment and values and root dry weight values increased with increasing wind speed for all soil types. For ontogeny stage one germinants, root growth was not affected by increasing wind speed to the same degree as shoot growth, provided the germinants were able to establish.

Total, shoot and root dry weight values of ontogeny stage two germinants grown in the sandy soil increased from the low to moderate wind speed and increased or changed little from the moderate to high wind speed treatments. The values of germinants grown in the finer textured soils generally decreased with increasing wind speed. Some of the differences were significant. There was little difference between wind speed treatments in the total dry weight increment of germinants grown on the sandy soil; however, increment generally decreased with increasing wind speed for the finer soil textures.

Shoot length increment of ontogeny stage two germinants for the sandy soil treatment increased from the low to moderate wind speed then decreased from the moderate to high wind speed. Responses for the finer textured soils increased with increasing wind speed. This is the only time that performance of the sandy loam and loamy sand soils was superior to that of the sandy soil. Shoot length values for all the soil types decreased with increasing wind speed.

Root growth of ontogeny stage two germinants in the finer textured soils was affected more by increasing wind speed than that in the sandy soil. For the sandy soil treatment, root length increment and values for ontogeny stage two germinants increased with increasing wind speed. For the finer soil types, they increased from the low to moderate wind speed then decreased or remained the same from the moderate to high wind speed.

For ontogeny stages three to five, germinants grown on the sandy soil were again affected less by increasing wind speed than those grown on the loamy sand and sandy loam soil. Total, shoot and root dry weight values for the sandy soil increased from the low to moderate wind speed and then changed little from the moderate to high wind speed treatments; whereas, those for the loamy sand and sandy loam soil treatments increased from the low to moderate wind speed then decreased from the moderate to high wind speed treatments. Total, shoot and root dry weight increment for the sandy soil increased from the low to moderate wind speed then changed little from the moderate to high wind speed. For the finer textured soils, the response varied with ontogeny stage. Increment increased from the low to moderate wind speed then decreased from the moderate to high wind speed for ontogeny stage three. For ontogeny stage four and five, increment increased from the low to moderate wind speed then remained the same and increased respectively from the moderate to high wind speed. In cases where the response decreased from the moderate to the high wind speed, the response for the high wind speed treatment was almost always

greater than or equal to that for the low wind speed treatment.

Shoot length values decreased with increasing wind speed for ontogeny stage three to five germinants grown in all soil types. The greatest reductions occurred between the moderate and high wind speeds. Ontogeny stage three and four germinants grown on the sandy loam and loamy sand soil type were affected the most. The reductions for ontogeny stage five germinants were not as great. The same trends do not occur for the root length data. For the sandy soil, as wind speed increased, the final root length of ontogeny stage three to five germinants increased. For the sandy loam and loamy sand soils, root length increased from the low to moderate wind speed treatments then decreased from the moderate to high wind speed treatments. For root growth, this is a continuation of the trend observed in ontogeny stage two. Again, the values for the sandy loam and loamy sand soil types at the low wind speed do not vary greatly from those at the high wind speed.

There was a small increase in height from the initiation of the experiment to the termination for ontogeny stages four and five and a large increase for ontogeny stages one to three, depending on wind speed and soil type. The younger stages "catch-up" to the older stages in terms of final height. This corresponds to the height increment trends, the greatest height increment occurring for ontogeny stage one and the least for ontogeny stage five. There is no similar trend for the root length. Differences in root length values between ontogeny stages at the start of the experiments remain at the termination of them.

For ontogeny stages three to five, root length increment and values of germinants grown in the sandy soil type increased with increasing wind speed. For the sandy loam and loamy sand soils, the same relationship holds for the increment but not the value data. Root length values increased from the low to the moderate wind speed treatment then decreased at the high wind speed treatment. Values at the high wind speed were similar to those at the low wind speed treatment.

4.5.3.4 STATISTICAL TESTS

Tests for normality and homoscedasticity were conducted using graphical means for both and the Burr-Foster Q-Test (Anderson and McLean, 1974) for the latter. The results of the Q- Test are presented in Table 14. According to Anderson and McLean (1974), if the calculated value is less than the critical value at p=0.01, do not transform, if it is larger than the critical value at p=0.001 transform and if it lies between the critical range, transform if there is a practical reason to do so, otherwise do not transform. For the ANOVA, variance was homoscedastic for the shoot dry increment and shoot length values only. All other response variables exceeded the p=0.001 critical value and transformations were conducted. ANOVA's for all response variables were conducted with the data transformed with the function giving the lowest Q-Test value. Tests for normality were based on computer generated Rankit plots. All response variables achieved normality. The results of the ANOVA on the response variables is presented in Table 15. See Appendix H for the full ANOVA tables.

Table 14. Results of the Burr-Foster Q-Test.

Trans-formation	Total Seedling Dry Wt.		Shoot Length		Root Length		Final Shoot Dry Wt. *		Final Root Dry Wt.*	
	Incr.** (mg/day)	Value** (mg)	Incr.** (mm/day)	Value** (mm)	Incr.** (mm/day)	Value ** (mm)	Incr.*** (mg/day)	Value** (mg)	Incr.*** (mg/day)	Value** (mg)
					Approximate Chi-square Values					
Y	130.64	294.23	252.84	**66.37***	95.99	104.74	**37.12***	192.44	92.52	435.74
$\sqrt{(Y+1)}$	111.84	133.70	186.16		80.47	**77.81**		93.11	88.66	249.13
Ln(Y+1)	96.05	**70.06**	129.05		**71.33**	82.31		**64.87**	**30.45**	119.14
1/(Y+1)	**73.18**	153.68	**74.50**		71.42	161.05		157.96	78.25	**52.24**

Values in **bold** type indicate the transformation used for that response variable.
* No further tests conducted, untransformed data meet assumptions of ANOVA.
** Critical range Chi square (p=0.01, 44 df)= 68.67; (p=0.001, 44 df)= 78.70
***Critical range Chi square (p=0.01, 26 df)= 44.97; (p=0.001, 26 df)= 53.33

Table 15. Results of the ANOVA on the response variables (measured at time of harvest) in the ontogeny experiment. All tests were conducted at p=0.05.

Source** of Variation	Total Seedling Dry Wt.		Shoot Length		Root Length		Final Shoot Dry Wt. *		Final Root Dry Wt.*	
	Incr. (mg/day)	Value (mg)	Incr. (mm/day)	Value (mm)	Incr. (mm/day)	Value (mm)	Incr. (mg/day)	Value (mg)	Incr. (mg/day)	Value (mg)
					Significance of F					
WS	nt ***	nt	nt	nt	nt	nt	nt	nt	nt	nt
ST	0.000	0.000	0.000	0.000	0.000	0.000	0.114	0.000	0.112	0.000
ONT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
WSxST	0.013	0.000	0.000	0.000	0.000	0.000	0.400	0.000	0.088	0.000
WSxONT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.168	0.000
STxONT	0.065	0.000	0.000	0.000	0.000	0.096	0.387	0.000	0.438	0.000
WSxSTx ONT	0.794	0.000	0.000	0.000	0.000	0.006	0.420	0.000	0.879	0.000

* ONT 1 and 2 not included in ANOVA for the increment data. ** WS- Wind Speed ST- Soil Type ONT- Ontogeny Stage. *** nt- No Test

5.0 DISCUSSION

5.1 GERMINATION STUDY

The objectives of the germination study were to determine the effects of various soil moisture potentials on seed germination and to observe the effects of continued drying on the germinants. These objectives were not achieved in either the preliminary or the main germination study because seed did not germinate in the wind tunnel, because the desired soil moisture potentials for sowing could not be predicted accurately, and because seed were sown when the soil was saturated only. Lack of germination and the inability to sow seed at desired soil moisture potentials precluded the observation of the effects of soil moisture stress on germination and of continued drying on the germinants.

The germination study experiments were made twice. In the first attempt, the preliminary germination study, untreated seed were sown and germination monitored. The seed did not germinate in the wind tunnel and were sown when the soil was saturated only. Soil moisture potentials could not be predicted accurately to enable sowing at other times. The results were analysed and the experiments modified. A new method was devised to predict the time when specific soil moisture potentials would occur and in this attempt osmotically primed and untreated seed were sown in the wind tunnel. This second attempt was called the main germination study.

Unfortunately the new proceedure also was not successful. Seed were not sown at the desired soil moisture potentials, except for those sown when the soil was saturated (Table 7). Again osmotically primed and untreated seed failed to germinate in the wind tunnel. Therefore, the seed were removed from the soil surface and placed in Petri-dishes in a growth chamber to check the seed for viability.

The growth chamber germination data are usefull. The germination characteristics of the seed have been influenced by the presowing treatment and by conditions encountered while in the wind tunnel. Differences in the growth chamber germination results make it possible to draw some conclusions on the effects of osmotic priming, wind speed and soil type on the water absorption by the seed and the effects on germination. Results for this portion of the thesis research are based entirely on the germination characteristics of the seed after being removed from the soil in the wind tunnel, placed in Petri-dishes and the germination process allowed to proceed in a growth chamber.

The results of the growth chamber germination tests for the main germination study, indicate that unprimed seed are affected more by their physical environment than primed seed. This is illustrated in Figure 10 (A-F) in which germination of wind tunnel sown seed is compared to germination of control,

primed and unprimed seed not subjected to the wind tunnel treatments. Germination of wind tunnel sown primed seed decreased only slightly below that of the control seed with each increase in wind speed; however, these decreases were minor compared to those observed for the unprimed seed. With each increase in wind speed, germination of the unprimed seed fell below that of the control seed, the magnitude of the effect varying with soil type. For example, germination of seed from the sandy soil was affected more by increasing wind speed than germination of seed from the loamy sand soil. The reduction in germinative capacity with increasing wind speed, the magnitude of the reduction varying with soil type indicates that some characteristic of the environment is affecting the unprimed seed. This factor does not have a similar effect on the primed seed.

It appears that osmotic priming negates the affects of the environment on primed seed. The main and most apparent difference between primed and unprimed seed is the amount of water the seed have absorbed before the growth chamber germination tests. The primed seed absorbed most the their water during the priming process with some additional water being absorbed from the soil surface in the wind tunnel. Any water absorbed by the unprimed seed would come from the soil surface.

Examination of the unprimed seed which did not germinate in the growth chamber tests revealed that most of the seed were sound. This indicates that the unprimed wind tunnel sown seed failed to germinate for some physiological or environmental reason. Although the seed were filled and sound, no test was conducted to determine if the seed were viable.

Based on the principles of osmotic priming, once a seed absorbs a quantity of water, the germination process begins. If subjected to drying, the germination process effectively stops where it is, awaiting the reintroduction of water to begin the process again. Therefore, theoretically, all the unprimed seed should have resumed and completed the germination process once placed in the Petri-dishes. This did not occur for all the seed. This may indicate that there is an adverse effect of partial wetting followed by drying on germination of untreated jack pine seed.

The difference in the response between soil type treatments for the unprimed seed and the lack of a similar effect on the primed seed would indicate that the cause for the reduced germinative capacity is the lack of absorption of a sufficient quantity of water. It is hypothesized that the seed may require a critical, minimum amount of water to reach a stage in the germination process from which, if they are dried and subsequently rewetted, they can resume germination without adverse effects. The environment may have affected the unprimed seed by limiting the amount of water available to the seed.

Russo (1978) conducted a Petri-dish wetting and drying study with jack pine. For all treatments (1-5 drying and wetting cycles) the germinative capacity of the treated seed was less than that of the controls. Although these differences were not statistically significant, the trends support those evident in this study.

The fact that the germinative capacity of the primed and unprimed seed was not similarily affected supports my hypothesis. The germinative capacity of the primed seed was not affected as wind speed increased. When osmotically primed, the primed seed absorbed the minimum amount of water during the

osmotic priming process. When dried and rewetted, their germinative capacity was not affected. The unprimed seed, which rely on the water they can absorb from the soil, were affected because they did not absorb the minimum amount of water before drying soil conditions became severe.

If this hypothesis is correct, then the soil moisture relations of the loamy sand soil should be superior to that of the other two soil types, since germinative capacity of seed from this soil was not affected until the highest wind speed. Seed placed on this soil type theoretically were able to absorb the minimum quantity of water at the low and moderate wind speeds such that germination was not affected.

Unfortunately, the soil moisture potential data collected during the main germination study do not support the hypothesis. The data show that the sandy and sandy loam soils had higher soil moisture potentials (less negative) at a given time than the loamy sand soil type (Figure 8 (A-C)). At the low wind speed, the soil moisture potential of the sandy loam fell well below that of the loamy sand soil type, probably the result of severe crusting of the soil surface.

Perhaps the water that is apparently available to the seed in the sandy and sandy loam soils is not getting to the seed? Characteristics of the soil, such as hydraulic conductivity, seed soil contact and soil surface microtopography, may be affecting the availability of water to the seed.

The presence of water in the soil is of no consequence if it cannot move at a rate sufficient to meet the evaporative demand of the atmosphere and the requirements of the seed. Therefore, hydraulic conductivity of the soil affects the amount of water absorbed by the seed. Saturated hydraulic conductivity was highest for the sandy soil (3.72×10^{-4} cm/sec) followed by the loamy sand (1.26×10^{-4} cm/sec) and the sandy loam soil (1.08×10^{-4}cm/sec) or decreased from the coarsest to the finest soils, respectively. Equipment to conduct unsaturated hydraulic conductivity tests was not available. Brady (1974) and Hillel (1982), however, note that when unsaturated, the hydraulic conductivity of finer soils is higher than that of coarse textured soils. The reduction in hydraulic conductivity as the soil becomes unsaturated and the soil matric potential decreases from 0 to -1 bar, may be of several orders of magnitude (down to 1/100,000) of its value at saturation (Hillel, 1982). Additionally, Hillel (1982) notes that when unsaturated, water in coarse textured soils is most often found almost entirely in capillary wedges at the contact points of the particles. If this is the case, then once the sandy soil was no-longer saturated, which it would be once the experiments started, water availability to the seed would be limited to that which was trapped in these wedges. Once the moisture in wedges nearest the seed were exhausted, further movement of moisture to the seed would be limited.

According to Figure 8 (A-C) the sandy soil may have a greater soil moisture potential (lower negative value) than the loamy sand soil; however, this greater soil moisture potential is probably the result of the water trapped in the wedges. The water in the 0-1 cm horizon cannot move to the seed, but is present in sufficient quantity in the horizon to influence the soil moisture potential measurements. The water trapped in the wedges did not evaporate rapidly since it could not move to the soil surface and the zone of evaporation. It did evaporate, finally, through the process of vapour diffusion.

The soil moisture potential curves (Figure 8 (A-C)) show that the sandy loam had a higher soil moisture potential at the moderate and high wind speeds than the loamy sand. But it also had a lower saturated hydraulic conductivity than the loamy sand. This lower hydraulic conductivity may be a disadvantage of the sandy loam. Jeglum (1979), in his watering study with black spruce, attributed the inferior germination on a clay substrate, as opposed to good germination on a sand substrate, to the inability of the clay substrate to supply moisture as readily to the seed. Scott (1966) made similar observations under field conditions. When in the wind tunnel, the surface of the sandy loam soil appeared visually dry sooner than the loamy sand soil. The hydraulic conductivity of the sandy loam may not have been sufficient to meet the evaporative demand of the atmosphere. Although the saturated hydraulic conductivity of the sandy loam soil is only slightly less than that of the loamy sand, this may have been sufficient to reduce the moisture supplying characteristics of this soil, especially when the soil was no-longer saturated. The result was that the surface of the sandy loam soil dried more quickly.

At the end of the experiments when the soils were being processed, the sandy loam soil was very dense and hard packed when dry. This may indicate that the packing procedures were so severe as to compact the soil. Compaction of the soil would reduce pore size and increase tortuosity and thus reduce the hydraulic conductivity of the soil.

Seed soil contact is also a critical determining factor in the moisture supplying capability of a soil. The seed soil contact for the sandy soil with its large particles and pores would be the poorest of all the soil types once the soil was dehydrated. Koller (1972) notes that the pores of a coarse textured soil are the first to drain as soil moisture is depleted and that relatively small reductions in soil moisture content may result in disproportionately large reductions in seed soil contact. This may be the case for the sandy soil. Although the graphs (Figure 8 (A-C)) show minor reductions in soil moisture potential relative to the other soils, these may result in major reductions in the seed soil contact. The loamy sand soil also has a large proportion of its sand fraction in large particles; however, relative to the sandy soil, it has a larger proportion of fine material which would reduce the pore size and improve the seed soil contact. It follows that the sandy loam soil should have, and probably does have the best seed soil contact. Its major hinderance may be its lower hydraulic conductivity due to smaller pore size.

The sandy loam soil exhibited crusting of the soil surface. The crust may have formed as a result of puddling caused by watering the soil surface before placing the pots in the wind tunnel. During puddling, the soil particles disperse in water and settle out in a differential rate. Clay particles settle out last and are oriented parallel to each other (Pritchett, 1979). These clay particles would effectively seal the pores, reducing contact of the seed with water columns in the soil. Although the sandy loam has a lower clay content than the loamy sand, it also has a larger fraction of its sand sized particles in the fine sand and very fine sand categories. With these smaller sand sized particles the sandy loam soil would have smaller pores which would be easier to plug than the pores of the loamy sand soil.

The microtopography of the soil surface has also been found to affect soil moisture availability to

the seed (Harper et al., 1965). After packing and watering the pots of loamy sand soil, it was observed that the finer particles would settle leaving the surface littered with small stones (the 15.4% of particles >2mm in diameter). When the seeding template was placed on the soil surface and the seed dropped through the holes, they would fall beside these stones if such a stone happened to occupy the position below the hole. The seed were then pressed into the soil surface where they lay. Harper et al. (1965) found that the heterogeneity of the soil surface did affect the water uptake and germination of seed in their study. Variations in the water absorption and germination of seed on different soil surfaces was attributed to variations in relative humidity in cracks on the soil surface (Harper and Benton, 1966). Seed were protected from excessive dessication. This may also be the case for the loamy sand soil type. The rough surface caused by the stones increased the relative humidity near the soil surface thus reducing the amount of dessication of the soil and the seed. Both the soil and the seed lose moisture to the atmosphere (Harper and Benton, 1966).

There is no direct evidence to verify the above arguments that the loamy sand soil has better physical characteristics for absorption of water by seed; however, the arguments present the possibility that the loamy sand soil does provide better soil moisture relations than the other two soil types. The above discussion illustrates the complex relationship between the seed and the soil, and illustrates the point that apparently minor differences between the soil types may result in differences in water absorption. Seed sown on the loamy sand soil type may have been able to absorb a sufficient amount of water to enable them to advance past the critical point of water absorption that would enable the seed to resume germination with no detrimental effects if rewetted. The other soil types could not provide the critical amount of water in the same time frame.

One possible reason for reduced germinative capacity of seed on the sand and sandy loam is that some jack pine seed may have entered a state of secondary dormancy induced by the absorption of a small quantity of water. Villiers (1975) notes that "Seed otherwise germinable may be caused to become dormant by imbibing them in unfavourable environmental conditions". Tran and Cavanagh (1984) note that "The mechanisms underlying secondary dormancy are still not fully understood but are assumed to be similar to those operating with dormancy in general... Factors such as temperature, absence of light or oxygen, presence of volatile or allelopathic inhibitors and moisture conditions have all been shown to contribute".

The induction of secondary dormancy in jack pine has never been proven (no literature found) and is not believed to occur since the species is generally regarded as not having primary dormancy. Jack pine seed occasionally exhibits some dormancy but usually germinates to capacity within 15 to 60 days (Rudolf, 1958). Under field conditions, however, jack pine does exhibit delayed germination. Kokocinski (1965), Scott (1970), Hacker et al. (1983), Smith (1984), and Thomas and Wein (1985b) cite examples were jack pine seed has germinated over a two to three year period under field conditions.

Unfortunately, the exact reason for the loss of germination capacity cannot be determined based on

these experiments. The results of these experiments serve only to raise questions about the possibility of a physiological characteristic of the seed which prevents it from germinating under optimal conditions after imbibing water for a short period of time and then being dried. Further research is needed. It must be noted that the results are based on one replication of the experiment at the whole plot level. Each wind speed was run only once. Additional replications would have verified the trends discussed.

It must be noted that the germinative capacity of primed and unprimed control seed are not significantly different. Under ideal conditions (no moisture stress and optimum temperature) osmotic priming does not affect the germinative capacity in any way. This reflects on the main purpose of osmotic priming which is to increase the rate of germination and make it more uniform.

The greatest advantage of osmotic priming occurs 72 hours after the start of the germination tests (Figure 10 (A-F)). By this time more of the primed seed have germinated than unprimed seed at all wind speeds. This advantage is especially apparent at the high wind speed. A comparison of the controls in Figures 10 (A-F) indicates that the primed seed have an inherent capability to germinate faster than the unprimed seed given optimum conditions.

It is uncertain why the primed seed failed to germinate in the wind tunnel, even at the low wind speed. The graphs of the preliminary germination test (Figure 9 (A,B)) suggested that the seed had imbibed a sufficient quantitiy of water to advance the germination process significantly. The priming treatment was supposed to duplicate this effect and theoretically allow the seed to begin germination from the point the seed in the preliminary study left off. Unfortunately, the preliminary germination curves and the control curves for the primed seed cannot be compared due to different environmental conditions in the growth chambers during the Petri-dish experiments. If the curves were comparable, then it would have been known if the priming treatment had advanced the germination process to the same point as in the preliminary germination study. The obvious reason why the seed did not germinate in the wind tunnel is because they did not absorb a sufficient amount of water to complete the germination process.

Another possible reason for the failure of the primed seed to germinate in the wind tunnel would be that the priming treatment was not optimal. Fleming and Lister (1984) tried 48 treatment combinations of imbibition time and temperature and solute concentration of which only two were optimal. In this study, the temperature and the osmotic potential of the priming solution were selected based on the results of the studies by Simak et al. (1984) and Fleming and Lister (1984). There was no time to conduct a study to determine the optimum priming treatment for jack pine.

The combinations selected were not optimum. When compared to controls, the germination rate of the primed seed was further advanced after being sown on the soil surface in the wind tunnel (Figures 10A and 10E). The seed absorbed an additional amount of water from the soil thus further advancing the germination process. Osmotic priming did not advance the germination process to the point where radicle emergence would occur with a minimal amount of water absorption. Further research to determine the optimum osmotic priming conditions is needed.

5.2 ONTOGENY STUDY

The objectives of the ontogeny study were to observe the effects of moisture stress on the morphological attributes of germinants at various stages of ontogeny and to determine the soil moisture potentials at which these germinants begin to die. Both objectives were achieved. The effects of drought on the performance (reflected in the response variables) of germinants at various stages of ontogeny will be discussed relative to components of the environment (soil type and wind speed).

It is evident from the data that soil type played a significant role in the response of different ontogeny stages to increasing wind speed. Ontogeny stages one and two, grown on the sandy loam and loamy sand soil types, were the most affected by increasing wind speed. At the high wind speed, ontogeny stage one germinants did not establish on either of these two soil types and establishment of stage two germinants was poor. This was not the case for the sandy soil treatment. Additionally, the more advanced the ontogeny stage the less effect increasing wind speed had on the germinants in a particular soil type. Germinants grown in the sandy soil were affected less by increasing wind speed than those grown on the other two soil types.

I believe that the texture and structure of the soil, soil moisture retention and hydraulic conductivity influenced the establishment and growth of the different ontogeny stages as wind speed increased. Additionally, the stage of ontogeny, and more specifically the root length, interacting with the soil characteristics, affected the performance of the germinants. Support for my hypothesis and the possible mechanisms of the effects of the above mentioned factors will be discussed.

The lack of sufficient or large enough macropores may have been the cause of poor establishment of ontogeny stage one and two germinants on the sandy loam and loamy sand soil types. The radicles of ontogeny stage one and some ontogeny stage two germinants grown on these soil types failed to penetrate the soil surface and in the latter case, continue penetration of the soil. This did not occur on the sandy soil.

Root penetration of the soil and root elongation is reduced as the number of continuous macropores (diameter $\geq$ 60 μm) decrease in the soil (Russell 1977; Kramer, 1983). This occurs mainly because roots are usually in excess of 60 μm in diameter and have difficulty penetrating pores smaller in diameter (Kramer, 1983).

The degree of radicle development and penetration into the soil at the start of the experiments of ontogeny stages one and two make them very susceptible to the number and distribution of continuous macropores in the soil. Although no tests were conducted, the number of macropores in the sandy soil are probably greater than the number in the loamy sand and the sandy loam soils because of the coarseness of the sandy soil relative to the other soil types. Additionally, a crust formed on the sandy loam and loamy sand soil types. This would have further reduced the number of macropores present in the surface of these soils.

Macropore availability alone cannot explain the poor establishment of ontogeny stage one germinants for the sandy loam and loamy sand soil treatments at the high wind speed, when at the low wind speed establishment of ontogeny stage one germinants on the same soil types was not affected. One would expect little difference in macropore availability between the same soil types prepared in similar ways for two wind speed treatments. The variation between the low and high wind speed would indicate that soil moisture must have some part to play in the establishment and growth of the ontogeny stage one and two germinants since the drying rate of the soil increased as wind speed increased (Figure 13 (A-C)). It is accepted that plant growth is affected directly by soil moisture stress; however, it can also be affected indirectly by the effect of soil moisture on soil structure.

Russell (1977) states that "Decreasing soil water potential causes soil strength to increase with the result that extending roots experience greater mechanical impedance...". Russell (1977) defines soil strength as the resistance of the soil to deformation. Decreasing water content increases strength due to the loss of the lubricating effect of water films between the soil particles. As the surface friction between adjacent particles increases, the resistance to deformation increases (Hillel, 1982). This influences root growth because the force which the roots must exert to penetrate the soil matrix increases as the soil drys. Soils used in these experiments demonstrated an increase in strength with drying. This was especially evident for the loamy sand and sandy loam soils which had a massive structure when dry.

Even if the number of macropores was limiting at the low wind speed, the better moisture relations of the loamy sand and sandy loam soils at this wind speed would reduce the resistance of the soil to radicle penetration and increase establishment. These soils would have less impedance for a period of time thus enabling the establishment and growth of ontogeny stage one germinants. Stage two germinants would also benefit from the reduced impedance.

Even when moist, however, the loamy sand and sandy loam soils had higher impedance than the sandy soil. The initial root length data (Table 11) show that root length of germinants on these soil types was consistently less than that on the sandy soil type. Soils in the supplementary test to determine initial germinant characteristics were kept moist; therefore, increased impedance as a result of soil drying could not occur. If reduced impedance is not the cause of the reduced growth, then possibly the presence of fewer macropores is the cause.

Once the germinants were established (i.e. the roots were in the soil) macropore availability and soil impedance did not appear to play a significant role in the growth and survival of the germinants. If it did then, theoretically, root length increment should have decreased with increasing wind speed, especially for the sandy loam and loamy sand soil types. For most ontogeny stages and soil types, the root length increment increased with increasing wind speed (Table 13).

If the root length increment data are interpreted at face value, the roots are growing faster under more stressful conditions. The data may be incorrect since Kaufmann (1945) found that daily root length growth of jack pine decreased from 3.2 mm to 1.2 mm as a consequence of a reduction in soil water capacity from

11 to 2 percent. Increases in growth as a result of increased wind speed, however, are not unheard of (Gates, 1968, 1975; Campbell, 1977; Grace, 1981; Rosenberg et al., 1983) and will be discussed in detail below.

There is a possibility that the root growth length increment data are incorrect. The supplementary test conducted to determine initial germinant characteristics may not have been accurate. Root lengths may have been longer at the start of the moderate and high wind speed runs than predicted by measurement from the supplementary test. Using the smaller predicted root length from the supplementary test would inflate the difference between the root length at the start and end of the runs such that when divided by a shorter survival time, the quotient would be greater at the high wind speed than at the low wind speed. I would be very surprised if this is the case since the increase in root growth rate with increasing wind speed is very systematic. The wind tunnel wind speed runs were not systematic, the moderate wind speed was run first followed by the high and the low wind speeds respectively. If initial height is used as measure of consistency between seedlings in the wind tunnel runs, the trends observed above do not match those for height. Additionally, there was little difference in soil bulk density between wind tunnel runs and, although the average number of sunshine hours (Table 3) increases with increasing wind speed, the greatest difference is only one hour. The pattern of change in sunshine hours, however, is not reflected in any pattern in the initial shoot heights of the germinants nor is it expected that a difference in day length of an hour would have a signficant effect on the germinants given the duration of the experiments.

There are several interesting trends evident in the ontogeny stage three to five data which suggest that the growth and survival of these germinants is affected by the rate of drying front advancement through the soil profile and the inability of root growth to keep up. Survival times for germinants grown on the sandy loam and loamy sand soil types were shorter at the high wind speed than at the low wind speed (Table 11). This was despite the fact that root length increment increased with increasing wind speed (Table 13). The germinants at the high wind speed, having a higher root length increment than those at the low wind speed, could not have died before those at the low wind speed unless the soil and atmospherical conditions were such that they surpassed the advantage of higher root length increment. Higher root length increment should be an advantage since the roots grow more rapidly deeper into the soil profile where moisture conditions are more favourable. Figure 11 shows that the sandy loam and loamy sand soil types dried faster at deeper depths with increasing wind speed. The rate of drying must have been faster than the root length increment to account for the earlier mortality of the germinants.

The soil drying rate alone cannot explain the shorter survival time of the germinants. Hillel (1982) notes that the amount and rate of water uptake by plants is dependent on the properties of the plant, properties of the soil and the meteorological conditions at the time. The specific properties of the plant and soil which he cites as being influential are the rooting depth, the rate of root extension and the relationships between soil hydraulic conductivity, diffusivity and matric suction, respectively. The meteorological conditions dictate the rate at which the plant must transpire and hence the rate at which it

must extract water from the soil in order to maintain its own turgor.

Not only did the germinants at the high wind speed have a shorter survival time than those at the low wind speed, they began to wilt and/or die at higher soil moisture potentials than those at the low wind speed (Table 11). At the high wind speed, the sandy loam and loamy sand soils may not have been able to provide a sufficient quantity of water to meet the transpiration rate of the germinant due to the rate of evaporation from the soil profile. Consequently, the germinants at the high wind speed died before and at a higher soil moisture potentials than those at the low wind speed. Unfortunately, in this research, many of the parameters needed to support these arguments were not collected. Of particular interest would have been the germinant moisture potential at which wilting or mortality occurred, the transpiration rates of the germinants, the unsaturated hydraulic conductivity of the soil and the evaporation rate of water from the soil at differenct wind speeds.

Further support for my hypothesis is found in the performance of germinants grown in the sandy soil. The time to harvest and the soil moisture potential at time of death did not change much between the low and high wind speed for the sandy soil treatment (Table 11). A major difference between the sandy soil and the other soil types is the soil moisture holding characteristics and therefore the drying characteristics of the soil.

Recall that as saturated coarse textured soils are drained the water capillaries break at higher soil moisture potentials. Once the capillaries are broken, the water is held mainly in the capillary wedges between the soil particles. Such water can only be lost by the slow process of vapour movement through the soil profile. As a result the drying front moves slowly into the soil profile. In contrast, as saturated finer textured soils drain, the capillaries stay intact at lower soil moisture potentials. Consequently, water is able to move through the soil profile to the soil surface and the zone of evaporation at lower soil moisture potentials. These relationships probably held for soils in this research. The fine textured soils (sandy loam and loamy sand) dried faster at the high wind speed than the coarser (sandy) soil (Figure 12).

Once the sandy soil was no longer saturated, the movement of water to the zone of evaporation ceased and the water was trapped in the capillary wedges. As the roots of the germinants in the sandy soil grew they encountered the water held in the capillary wedges. As long as the roots were able to elongate, they probably encountered enough water in the capillary wedges to meet the transpiration rate of the germinant. Eventually the water was lost from the sandy soil through the processes of vapour diffusion and transpiration; however, water loss through these processes is slower than through the process of evaporation from the soil surface. The germinants were able to survive longer and grow larger in the sandy soil than the other soil types. It appears that under stressful conditions and in the absence of a water table, the sandy soil may be better for the establishment, growth and survival of germinants at early stages of development.

The results of this study add to the controversy of the legitimacy of the permanent wilting point as a soil constant. It is generally accepted that plants begin to wilt and eventually die when the soil reaches

the permanent wilting point (-15 bars) (Kramer, 1982). This did not occur for the high wind speed treatment in this research. Kramer (1983) and especially Hillel (1982) present arguments from the literature which note that wilting is dependent not on the soil alone but on characteristics of the plant, on meteorological factors affecting the rate of transpiration, and on soil factors affecting the rate of absorption. This was observed in the results of this research.

There is some indication in the total dry weight and root length value data that an increase in wind speed is not detrimental to germinant growth provided the soil moisture conditions are favourable for a length of time. For the loamy sand and sandy loam soil treatments, total dry weight and root length values increased from the low to the moderate wind speed; after which, the values decreased from the moderate to the high wind speed (Tables 12 and 13). For the sandy soil, the values increased from the low to moderate wind speed then changed little from the moderate to high wind speed.

Wadsworth (1959) and Morse and Evans (1962) (both cited in Grace, 1977) found that there was an optimum wind speed for plant growth in their experiment with agricultural species given the optimum soil moisture conditions they used. These responses were attributed to the effects of wind on photosynthesis. Grace (1977) cites several studies in which an increase followed by a decrease in net photosynthesis was observed with increasing wind speed. The trends observed by Wadsworth and by Morse and Evans are similar to those for germinants in this research.

Grace (1977) felt that the reduction in growth at a certain wind speed in Wadsworth's (1959) study was due to the inability of the soil to supply water rapidly enough to keep pace with the loss from the leaf. The variable responses from the different soil types in this study could have had similar effects as in Wadsworth's study. Each soil type would be able to supply a quantity of water dependent on that soil's physical characteristics and the severity of the environmental conditions.

It is generally believed that increases in wind speed increase transpiration with the inevitable effect of reducing leaf water potential thus causing stomatal closure. With stomatal closure comes a corresponding decrease in photosynthesis (Kramer and Kozlowski, 1979) and the production of metabolites necessary for seedling growth. If these statements are true then germinant growth should decrease with increasing wind speed. It has been suggested through modelling and experimentation that an increase in wind speed can cause a decrease in transpiration (Gates, 1968, 1975; Campbell, 1977; Grace, 1981; Rosenberg et al., 1983). The main effect of wind is to cool the leaf thereby reducing the vapour pressure in the substomatal cavities and reducing the driving gradient between the vapour pressure in the substomatal cavities and the air. This reduction in driving gradient results in a reduction in water loss from the leaf, open stomates and continued respiration.

It is uncertain whether wind had such an effect on the germinants in this study since no measurements of transpiration nor leaf temperature were taken; however, the growth trends cannot be ignored. Despite problems with the experimental procedure (the lack of initial measurements of germinant attributes) and the experimental apparatus (lack of consistent light intensity between runs) the magnitude

in difference of the response variables between the runs suggests strongly that increasing wind speed is not entirely detrimental to the germinants depending on soil type.

It can be argued that the differences in response with increasing wind speed may be due to initial differences between the germinants at the start of the wind tunnel runs. Differences would have to be very large to account for the magnitude of increase as wind speed increases for some of the ontogeny stages, especially for the sandy soil type. Differences between germinants at the start of the runs were probably not major due to the maintenance of similar growing conditions in the greenhouse for all the wind speed runs. An indication of the similarity between wind speed runs for a soil type may be gained from the heights of the germinants (Table 13). Heights were measured before the start of each run. Differences between wind speeds within soil types and ontogeny stages range from 3-5 mm. Statistically, some of these differences are significant, whether they are physiologically significant is unknown.

Because the wind tunnel was located in the greenhouse, the amount of sunshine the germinants received in each wind tunnel run would be very dependent on weather conditions at the time of the run. Table 3 shows that the mean number of sunshine hours per day increased from the low to the high wind speed run. It is doubtful that a difference in light intensity between wind tunnel runs caused an increase in total dry weight with increasing wind speed. The increase in sunshine hours between the low and the moderate wind speed was 0.3 hours (18 minutes) per day. It is doubtful that an 18 minute difference in sunshine hours per day could account for the magnitude of difference in the total dry weight and root length values observed between the low and the moderate wind speed.

The effects of bulk density on root growth in different wind speed runs can be dismissed as an influential factor. The bulk density for the sandy soil type (Table 11) was identical at the low and high wind speed yet root length values were not.

It is interesting that there was very little difference in the final height of germinants between ontogeny stages and wind speed treatments (Table 13). Except for ontogeny stage one at the moderate wind speed and stages one and two at the high wind speed, the younger stages "caught-up" to the older stages in terms of height. The "catch-up" in height is probably a reflection in the change in growth activities of the germinants. Height increment was greater for ontogeny stage one germinants than for ontogeny stage five germinants (Table 13). Most of the hypocotyl extension of ontogeny stages four and five took place outside the wind tunnel under optimum environmental conditions before the experiments began. When placed in the wind tunnel these ontogeny stages are just completing hypocotyl extension and beginning epicotyl growth respectively. This compares to ontogeny stages two and three in which hypocotyl extension was the most active stage of germinant development when they were placed in the wind tunnel.

Although the younger ontogeny stage caught up in height this does not mean that the germinants were as well developed. Although the germinants of different ontogeny stages are approximately similar in height, the shoot dry weight data (Table 12) show that the germinants are numerically different in weight.

The difference in weight probably corresponds to the difference in the production of epicotyl needles.

The data indicate that jack pine germinants attain a specific height before epicotyl development begins and that the inability to attain this height (hypocotyl extension) occurs only at the most severe moisture conditions. The loamy sand and sandy loam soil types at the high wind speed are considered the most severe environmental conditions for germinant growth and survival due to the soil physical characteristics and moisture conditions affecting growth .

5.3 APPLICATION OF RESULTS TO THE FIELD

There are often problems when attempting to apply the results of greenhouse or growth chamber studies to field conditions since few, if any, of these types of experiments can reflect the variablility of conditions encountered in the field. The results, however, can be applied as long as one realizes that problems exist. The results of this research are no exception. I will make a few suggestions, based on the results of my research, regarding direct seeding of jack pine.

There are pros and cons in using osmotically primed seed in direct seeding projects. Osmotic priming enhances the speed at which jack pine will germinate. The rapid germination of primed seed and hence rapid establishment of a root system would be advantageous to jack pine survival. The roots are deep in the soil profile where moisture relations are more favourable.

Osmotic priming, however, eliminates the delay in germination exhibited by unprimed seed thus eliminating the staggered germination currently displayed in the field (Kokocinski, 1965; Scott, 1970; Hacker et al., 1983; Smith, 1984; Thomas and Wein, 1985b). Kokocinski (1965) felt that delayed germination, which he called 'dormancy', would be an advantage in terms of a survival stategy for the species. This is supported by Thomas and Wein (1985b) who feel that the delayed emergence from the soil is a survival strategy which may increase the probability of establishment of jack pine even if the immediate conditions are inhospitable (Thomas and Wein, 1985b). Primed seed would germinate rapidly and hence would be susceptible to adverse environmental conditions should they occur before the germinants became adequately established. No reserve of seed would remain for germination the next year when environmental conditions may be more favourable.

The rate of germination of the primed seed in this study does not reflect the potential of primed jack pine seed. The priming treatment levels selected were not optimum. Further research to determine the optimum priming treatments may accelerate germination to the point that the loss of the effect of delayed germination may be overshadowed by the rapid establishment of the germinants.

Until field trials are conducted with osmostically primed seed, it is uncertain whether there would be any biological or economical advantages of sowing primed seed. Biologically, there may or may not be an advantage given the result that osmotically primed seed do not display delayed germination but germinate faster than unprimed seed. Economically, the additional costs of treating the seed must be considered

relative to any advantages in establishment gained in the field. Additionally, there is no commercially available apparatus for priming the large quantities of seed required for a direct seeding project on an operational scale.

Based on the combined results of the germination and ontogeny studies, a silviculturalist can expect that germination of untreated jack pine seed sown on finer textured soils should be better than on coarser textured soils since more water is available for imbibition. However, if environmental conditions become severe, establishment, growth and survival will be poorer on fine textured soils than on coarse textured soils. If untreated jack pine seed are direct seeded on coarse textured soils, the silviculturalist can expect poor germination the first year, but as a result of delayed germination, germination should increase over time. If environmental conditions become severe, establishment, growth and survival of jack pine will be better on the coarser textured soils than on the finer textured soils. These scenarios are dependent on environmental conditions.

To account for the inability to predict the environmental conditions after seeding, a silviculturalist could seed finer textured soils at a higher rate. This would provide more germinants and the possibility of more survivors should conditions become severe. It would, however, result in a severly overstocked stand should conditions be favourable after seeding. On coarse textured soils, the silviculturalist will have to be patient, since germination will probably occur over a two to three year period. A method of attaining good germination, establishment, growth and survival on all soil texture types may be through the use of seeding shelters. The shelters reduce the soil water loss in the vicinity of the seed thus reducing the variable effects that soil type has on germination, establishment, growth and survival of germinants.

6.0 CONCLUSIONS

This study indicates that unprimed jack pine seed are affected more by their physical environment than primed seed. Athough no seed germinated in the wind tunnel, germination trends of the unprimed seed taken from the wind tunnel and placed in Petri dishes in a growth chamber showed that there was a reduction in germinative capacity for some soil types with each increase in wind speed. The primed seed displayed no similar reduction in germinative capacity. Osmotic priming appeared to negate the effects of the environment on the germinative capacity of jack pine.

The exact reason for the loss of germinative capacity with increasing wind speed of the unprimed wind tunnel sown seed cannot be determined based on these experiments. The results of these experiments serve mainly to raise questions about the possibility of a physiological characteristic of the seed which prevents it from germinating under optimum conditions after imbibing water for a short period of time and then being dried. The fact that primed seed are not affected by increasing wind speed to the same degree as unprimed seed suggests that the cause of the reduced germinative capacity of unprimed seed may be the lack of absorption of a critical minimum amount of water. The primed seed receive this critical amount of water during the priming process whereas the unprimed seed must obtain the critical amount from the soil surface.

Germination results indicate that the loamy sand soil is better for jack pine seed imbibition than the sand and the sandy loam soils possibly due to the combined effects of better seed soil contact, soil hydraulic conductivity and soil microtopography. The loamy sand soil may have provided the critical, minimum amount of water for germination.

The osmostic priming treatment was not optimal. When compared to controls, the germination rate of the primed seed was further advanced after being sown on the soil surface in the wind tunnel. Osmotic priming did not advance the germination process to the point where radicle emergence would occur with a minimal amount of water absorption. Further research is needed.

The number of macropores in a particular soil type and the rate of drying of the soil were probably the major factors affecting establishment of ontogeny stage one and two germinants. Germinants were able to establish better at the low wind speed than at the moderate and high wind speed on the loamy sand and sandy loam soils due to the length of time the soil stayed moist and hence had less impedance and better moisture relations. This occured despite the fact that these soils probably had fewer macropores. Establishment on the sandy soil was not affected at any wind speed probably due to the greater number of macropores present in this soil.

Macropore availability and soil impedance probably did not play a significant role in the growth and survival of ontogeny stages three to five. It was felt that these factors were not significant once germinants were established since root length increment did not decrease with increasing wind speed as one would expect.

Several trends in the data lead to the conclusion that the growth and survival of ontogeny stage three to five germinants grown on the sandy loam and loamy sand soil types were affected by the rate of drying front advancement through the soil profile and the inability of root growth to keep up. The transpiration rate of the germinants probably played a significant role in the survival time since the germinants at the high wind speed died at higher soil moisture potentials than those at the low wind speed. The soil could not supply a sufficient quantity of water to the germinant to keep pace with the transpirational demand.

The sandy soil may have been better for the establishment, growth and survival of germinants at early stages of development because the water is held in the capillary wedges between the soil particles and does not rapidly evaporate from the soil profile. As long as the roots are able to elongate, they encounter pockets of water which may be sufficient to meet the transpiration rate of the germinant.

The data suggest that the permanent wilting point of -15 bars is not a soil constant which describes the point at which plants begin to wilt. In this research, germinants began to wilt and/or die at soil moisture potentials above the permanent wilting point. This supports the arguments in the literature that wilting is not dependent on the soil alone but on characteristics of the plant, on meteorological factors affecting the rate of transpiration, and on soil factors affecting the rate of absorption.

Increases in wind speed may not be detrimental to germinant growth provided the soil moisture conditions are favourable for a length of time. As wind speed increased from the low to moderate wind speed, total dry weight and root length increment increased for all soil types. From the moderate to high wind speed, these growth parameters decreased or changed little depending on soil type.

Jack pine germinants attain a specific height before epicotyll development begins and the inability to attain this height (hypocotyll extension) occurs only at the most severe moisture conditions (the loamy sand and the sandy loam soil types at the high wind speed).

Until such time as field trials are conducted using osmotically primed seed, it is uncertain whether their would be any biological or economical advantages of sowing primed seed. The rapid germination may or may not be an advantage given environmental conditions at the time of or shortly after sowing. Additionally, there is no commercially available apparatus for priming the large quantities of seed required for a direct seeding project on an operational scale.

7.0 RECOMMENDATIONS

7.1 WIND TUNNEL

Despite the good performance of the wind tunnel, several recommendations to improve the apparatus are given below:

1. The wind tunnel must be placed in a permanent location. Because the unit is made of wood, continued assembly and transport has resulted in and will result in damage. Additionally, the location should not be in the glass house of the greenhouse complex since environmental conditions are such that the unit cannot operate when it is hot and the high humidity of the glasshouse will damage the body of the unit. A room with adequate temperature control would be ideal. Natural light will not be required due to a recommendation below for artificial light. The permanent location will also allow the following modifications to be conducted without the worry of additional weight making the unit less portable.
2. The wind tunnel should be fitted with fluorescent or other lighting units to allow for the control of photoperiod and light levels. Very high output (VHO) fluorescent units would probably be best since they provide a high light intensity and fewer of these lighting units as compared to conventional units would be required. The system should be designed such that several lighting levels could be set depending on the desires of the researcher. Timers should be used to control the units.

   Because artificial lighting will be used, the plexiglass walls of the working section can be replaced with plywood or some other material. This will allow the working section to be insulated and thus reduce the heat load on the cooling system of the wind tunnel, allowing for better control of temperatures within the wind tunnel. Additionally, the interior walls of the working section could be painted white, thus allowing the reflection of the light back onto the interior of the wind tunnel. Plexiglass viewing ports can be installed in the wall at intervals to allow for observation of the contents without having to open the doors. The doors would also have to be modified to enable easy opening and access to the interior of the wind tunnel.
3. Better temperature and humidity control equipment should be installed. Units allowing more precise control of conditions within the wind tunnel may be required by other researchers. The present unit controls temperature by cycling all the heating elements off and on. Units which allow the heat intensity of the elements to vary or a system with many smaller coils that are switched off and on as required may be better. If such equipment cannot be obtained, the present system (thermostat and coils) could be used provided that the current relays are replaced with heavy duty units that can cycle off and on more often. The current thermostat will cycle off and on more often if the cover is removed. More frequent cycling of the heating coils results in a smaller temperature range around the set value. The

cover was left on for these experiments because it was feared that the frequent cycling would cause the relays to burn-out.

The present system of mist nozzles should be replaced with humidifiers which produce a finer mist and can cycle more accurately under the control of a humidistat. The current humidistat should be replaced with a higher precision unit. Modification of the humidity control system will enable the removal of the drip pans below the mist nozzles. There is some evidence that the drip pans are causing wind speed variability within the working section of the wind tunnel.

4. The fan and motor assembly for wind speed control should be modified. The fans need to be isolated from the body of the wind tunnel to reduce the vibration of the working section. The motor assembly with the stepped pulley speed control system should be replaced with a DC variable speed motor. This will allow infinite speed control and for automatic timer control of wind speed. The current system requires manual adjustment of the three wind speeds available. Without these modifications, if other wind speeds are required the pulley ratios must be changed before each run.

7.2 EXPERIMENTAL PROCEDURES

The following section presents some modification to the exprimental procedures if the experiments were to be repeated.

1. Three, more distinct soil texture types should be selected for the experiments. A consideration when selecting soil types is the ease to which the soil lends itself to processing when dry. The massive nature of clays or soils with a high clay component may disqualify these soils due to their tendancies to dry to solid, rock like masses.
2. The pots should be filled with soil in a manner that will yield more uniform bulk densities between pots of the same soil type within and between runs. In order to ensure this consistency the soils should be air dryed before being packed. This would ensure that soil moisture was not affecting the friction between soil particles and thus the resistance to compression. Soil in the pots should be compressed with a mechanical device equiped with some means of applying consistent pressure to the soil in each pot. A disk dropped from a fixed height or a lever assembly with a spring scale attached should be used. The proper drop height and weight of the disk or pressure on the lever (in the units of the scale) would need to be determined for the desired bulk density for each soil type.
3. More detailed physical and chemical analysis of the soil types should be conducted. Tests of macro- and micro-pore space for each run of the study and more frequent soil nutrient analyses during each run should be made.
4. In the germination study the time for the soil to reach a specified soil moisture potential was difficult to determine. One method of determining this more precisely would be to repack and place the pots in

pans of water for several hours. The water in the pans should be maintained at a constant level to ensure that each pot can receive the same amount of water. The pots should then be removed from the pans and allowed to stand and drain. After the pots are placed in the wind tunnel and the wind tunnel turned on, samples from certain pots should be taken at intervals. No seed should be sown. Only a certain number of pots should be sampled. From these samples a soil drying curve can be drawn and the proper sowing times for certain soil moisture potentials determined. The pots would then be removed from the wind tunnel, rewetted, ensuring thorough wetting of the entire soil mass, placed back in the wind tunnel and the experiments started. In this way the proper dry down time for that particular run of the wind tunnel can be determined.

5. For the ontogeny study, seedlings should be grown in a growth chamber to reduce the differences in initial seedling characteristics at the start of each run.
6. Extra pots of seedlings should be sown at the start of each experiment and then harvested before each wind tunnel run began in order to obtain initial seedling characteristics. Additionally, samples of seedlings should be taken during the wind tunnel runs to determine the progress of seedling growth. Such measurements would allow for the calculation of relative growth rate, a more representative measure of seedling growth.

7.3 OTHER RESEARCH

Based on the results of this research, many interesting trends were described and discussed. Due to problems in the experimental procedure these trends do not prove some stated hypotheses directly. As a result, this research should be repeated in part or in whole, and modified, heeding those recommendations given above, in order to verify some of the hypotheses. Some suggestions for additional research are given below.

A soil rewetting study should be conducted as part of the germination study in the wind tunnel to determine the effects of additional water on the seed. Unprimed seed did not germinate in this study when sown on saturated soil but did absorb enough water to advance the germination process within the seed. What additional quantity of water would be required to complete the germination process? What would be the effect of different rewetting intervals? How do soil type, rate of drying and seed treatment interact to affect germination under different water regimes?

Of major importance would be an experiment to investigate the possibility of moisture stress induced secondary dormancy of jack pine. Evidence in the study supports the hypothesis that there is a threshold amount of water which the seeds must absorb before they will not be adversely affected by a subsequent dry period. Some means to precisely control moisture to the seed would be required to simulate the minimal amount of water the seeds probably absorbed when on the soil surface.

A study to determine the optimum priming treatment for jack pine should be conducted. The optimum priming treatment should advance the germination process within the seed such that, with the addition of a small quantity of water, the seed would germinate rapidly. The present treatment was not optimal since the seed did not germinate in the wind tunnel and demonstrated faster germination rates than controls after being removed from the soil and rewetted in the Petri-dishes. Faster germination rates would mean even faster initial establishment after seeding and would enable the seedling to become well established before adverse environmental conditions occur. After determining the optimum priming treatment in the lab, wind tunnel tests should be conducted in conjunction with field studies to observe the response of primed and unprimed seed to a variety of simulated and actual environmental conditions respectively. If osmotic priming proved successful, additional research into an apparatus that would allow large quantities of seed to be primed successfully should be conducted.

Ontogeny experiments similar to those conducted for this thesis research but with more control of environmental conditions and with more detailed analysis of what is happening within the seedling (i.e. seedling moisture potential, stomatal conductance) should also be conducted. Such information would aid in determining what is happening to the seedling physiologically as moisture stress increases.

Rewatering studies should also be conducted on the germinates in experiments similar to the germination study. Germinants could be grown as in this thesis research and watered at varying intervals, to observe the effects of such treatments on the various stages of development. Care should be taken to avoid formation of "crusts" at soil surfaces since "crusting" appeared to play a role in germinant establishment.

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APPENDICES

APPENDIX A
LINEAR MODELS AND EXPECTED MEAN SQUARES TABLE
MAIN GERMINATION STUDY

ALL WIND SPEEDS COMBINED
Linear Model

$$Y_{ijkl} = \mu + W_i + \partial + S_j + WS_{ij} + T_k + WT_{ik} + ST_{jk} + WST_{ijk} + E_{(ijk)l}$$

where: μ is the grand mean
W is the i-th wind speed
∂ is the restriction error associated with running one wind speed at a time
S is the j-th soil type
T is the k-th seed treatment
E is the experimental error associated with the l-th replication of the jk-th treatment combination in the i-th wind speed

i= 1,2,3 Fixed Factor
j= 1,2,3 Fixed Factor
k= 1,2 Fixed Factor
l= 1,2,3 Random Factor

Expected Mean Squares Table

	3 F i	3 F j	2 F k	3 R l	
W_i	0	3	2	3	$Ó^2 + 18Ó^2(\partial) + 18Ø(W)$
$\partial(i)$	1	3	2	3	$Ó^2 + 18Ó^2(\partial)$ (restriction error)
S_j	3	0	2	3	$Ó^2 + 18Ø(S)$
WS_{ij}	0	0	2	3	$Ó^2 + 6Ø(WS)$
T_k	3	3	0	3	$Ó^2 + 27Ø(T)$
WT_{ik}	0	3	0	3	$Ó^2 + 9Ø(WT)$
ST_{jk}	3	0	0	3	$Ó^2 + 9Ø(ST)$
WST_{ijk}	0	0	0	3	$Ó^2 + 3Ø(WST)$
$E_{(ijk)l}$	1	1	1	1	$Ó^2$

WIND SPEEDS ANALYSED INDIVIDUALLY
Linear Model

$$Y_{ijk} = \mu + S_i + T_j + ST_{ij} + E_{(ij)k}$$

where: μ is the grand mean
S is the i-th soil type
T is the j-th seed treatment
E is the experimental error associated with the k-th replication of the ij-th treatment combination of soil type and seed treatment

i= 1,2,3 Fixed Factor
j= 1,2 Fixed Factor
k= 1,2,3 Random Factor

APPENDIX A continued
LINEAR MODELS AND EXPECTED MEAN SQUARES TABLE
MAIN GERMINATION STUDY

WIND SPEEDS ANALYSED INDIVIDUALLY continued
Expected Mean Squares

	3 F i	2 F j	3 R k	
S_i	0	2	3	$\sigma^2 + 6\phi(S)$
T_j	3	0	3	$\sigma^2 + 9\phi(T)$
ST_{ij}	0	0	3	$\sigma^2 + 3\phi(ST)$
$E_{(ij)k}$	1	1	1	σ^2

WIND TUNNEL VS CONTROL SEED
Linear Model

$$Y_{ij} = \mu + T_i + E_{(i)j}$$

where: μ is the grand mean
T is the i-th seed and soil type treatment combination or control of each seed treatment (seed not sown in the wind tunnel).
E is the experimental error associated with the j-th replication of the i-th seed and soil type treatment combination or control (unequal replication in this model)

i= 1,2,3,...,8	Fixed Factor
j= 1,2,3	Random Factor (For the soil type x seed treatment combination)
j= 1,2,3,4	Random Factor (For the control (primed and unprimed seed taken from cold storage))

Expected Mean Squares Table

	3 F i	3(4) R j	
T_i	0	3(4)	$\sigma^2 + 3(4)\phi(T)$
$E_{(i)j}$	1	1	σ^2

COMPARISON BETWEEN CONTROLS
Linear Model

$$Y_{ijk} = \mu + S_i + \partial + T_j + ST_{ij} + E_{(ij)k}$$

APPENDIX A continued
LINEAR MODELS AND EXPECTED MEAN SQUARES TABLE
MAIN GERMINATION STUDY

COMPARISON BETWEEN CONTROLS continued

where: μ is the grand mean
S is the i-th seedlot/time (seed prepared for each wind speed run)
∂ is the restriction error associated with preparing one seedlot at a time
T is the j-th seed treatment
E is the experimental error associated with the k-th replication of the j-th seed treatment in the i-th seedlot/time

i=1,2,3 Fixed
j=1,2 Fixed
k=1,2,3,4 Random

Expected Mean Squares Table

	3 F i	2 F j	4 R k	
S_i	0	2	4	$\sigma^2 + 8\sigma^2(\partial) + 8\emptyset(S)$
∂	1	2	4	$\sigma^2 + 8\sigma^2(\partial)$ (Restriction Error)
T_j	3	0	4	$\sigma^2 + 12\emptyset(T)$
ST_{ij}	0	0	4	$\sigma^2 + 4\emptyset(ST)$
$E_{(ij)k}$	1	1	1	σ^2

APPENDIX B

ANOVA TABLES
MAIN GERMINATION STUDY
I FULL MODEL- ALL WIND SPEEDS COMBINED

ANALYSIS OF CUMULATIVE GERMINATION PERCENT AT INDICATED TIME AFTER START OF GROWTH CHAMBER GERMINATION TEST

48 Hours — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.2296	0.1148	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil	2	0.0785	0.0393	1.0511	0.360
Seed Treatment	1	0.2570	0.2570	6.8820	0.013
Wind SpeedxSoil	4	0.1574	0.0393	1.0536	0.393
Wind SpeedxSeed Treatment	2	0.2266	0.1133	3.0340	0.061
SoilxSeed Treatment	2	0.0287	0.0143	0.3842	0.684
Wind SpeedxSoilxSeed Treatment	4	0.3026	0.0756	2.0258	0.111
Error	36	1.3443	0.0373		
Total	53	2.6245			

72 Hours — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.7792	0.3896	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil	2	0.0559	0.0280	1.0982	0.344
Seed Treatment	1	1.1551	1.1551	45.3576	0.000
Wind SpeedxSoil	4	0.0803	0.0201	0.7877	0.541
Wind SpeedxSeed Treatment	2	0.4147	0.2074	8.1417	0.001
SoilxSeed Treatment	2	0.0001	0.0000	0.0009	0.999
Wind SpeedxSoilxSeed Treatment	4	0.1493	0.0373	1.4655	0.233
Error	36	0.9168	0.0255		
Total	53	3.5514			

96 Hours — Transformation Used: None Required

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	3158.0507	1579.0253	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil	2	1580.0579	790.0290	5.6071	0.008
Seed Treatment	1	2495.6000	2495.6000	17.7122	0.000
Wind SpeedxSoil	4	632.2840	158.0710	1.1219	0.361
Wind SpeedxSeed Treatment	2	655.6637	327.8318	2.3267	0.112
SoilxSeed Treatment	2	756.0470	378.0235	2.6830	0.082
Wind SpeedxSoilxSeed Treatment	4	304.2574	76.0643	0.5399	0.707
Error	36	5072.3005	140.8972		
Total	53	14654.2612			

APPENDIX B continued

ANOVA TABLES
MAIN GERMINATION STUDY
I FULL MODEL- ALL WIND SPEEDS COMBINED

168 Hours — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.2063	0.1031	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil	2	0.3440	0.1720	4.8278	0.014
Seed Treatment	1	0.0967	0.0967	2.7145	0.108
Wind SpeedxSoil	4	0.2470	0.0617	1.7332	0.164
Wind SpeedxSeed Treatment	2	0.2025	0.1013	2.8421	0.071
SoilxSeed Treatment	2	0.1040	0.0520	1.4594	0.246
Wind SpeedxSoilxSeed Treatment	4	0.0513	0.0128	0.3598	0.836
Error	36	1.2825	0.0356		
Total	53	2.5342			

APPENDIX B
ANOVA TABLES
MAIN GERMINATION STUDY
II WIND SPEEDS ANALYZED INDIVIDUALLY

ANALYSIS OF CUMULATIVE GERMINATION PERCENT AT INDICATED TIME AFTER START OF GROWTH CHAMBER GERMINATION TEST

48 HOURS

Low Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.03040	0.01520	0.36582	0.701
Seed Treatment	1	0.00228	0.00228	0.05487	0.819
SoilxSeed Treatmen	2	0.02395	0.01198	0.28821	0.755
Error	12	0.49860	0.04155		
Total	17	0.55523	0.03266		

Moderate Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.13382	0.06691	1.08350	0.369
Seed Treatment	1	0.09029	0.09029	1.46211	0.250
SoilxSeed Treatmen	2	0.11338	0.05669	0.91801	0.426
Error	12	0.74104	0.06175		
Total	17	1.07853	0.06344		

High Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.07165	0.03583	4.10837	0.044
Seed Treatment	1	0.39099	0.39099	44.83830	0.000
SoilxSeed Treatmen	2	0.19393	0.09697	11.11984	0.002
Error	12	0.10464	0.00872		
Total	17	0.76121	0.04478		

72 HOURS

Low Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.00940	0.00470	0.18887	0.830
Seed Treatment	1	0.20008	0.20008	8.04018	0.015
SoilxSeed Treatmen	2	0.05361	0.02681	1.07715	0.371
Error	12	0.29862	0.02489		
Total	17	0.56171	0.03304		

APPENDIX B continued

ANOVA TABLES
MAIN GERMINATION STUDY
II WIND SPEEDS ANALYZED INDIVIDUALLY

Moderate Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.12614	0.06307	3.14891	0.080
Seed Treatment	1	0.07684	0.07684	3.83641	0.074
SoilxSeed Treatment	2	0.01128	0.00564	0.28159	0.759
Error	12	0.24035	0.02003		
Total	17	0.45461	0.02674		

High Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.00064	0.00032	0.01016	0.990
Seed Treatment	1	1.29292	1.29292	41.06137	0.000
SoilxSeed Treatment	2	0.08444	0.04222	1.34085	0.298
Error	12	0.37785	0.03149		
Total	17	1.75585	0.10329		

96 HOURS

Low Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.01410	0.00705	0.56008	0.585
Seed Treatment	1	0.01165	0.01165	0.92552	0.355
SoilxSeed Treatment	2	0.01079	0.00540	0.42860	0.661
Error	12	0.15105	0.01259		
Total	17	0.18759	0.01103		

Moderate Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.36410	0.18205	4.64888	0.032
Seed Treatment	1	0.25232	0.25232	6.44331	0.026
SoilxSeed Treatment	2	0.01910	0.00955	0.24387	0.787
Error	12	0.46992	0.03916		
Total	17	1.10544	0.06503		

High Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.05914	0.02957	1.30327	0.307
Seed Treatment	1	0.22766	0.22766	10.03386	0.008
SoilxSeed Treatment	2	0.11567	0.05784	2.54901	0.120
Error	12	0.27227	0.02269		
Total	17	0.67474	0.03969		

APPENDIX B continued

ANOVA TABLES
MAIN GERMINATION STUDY
II WIND SPEEDS ANALYZED INDIVIDUALLY

168 HOURS

Low Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.01311	0.00656	0.23109	0.797
Seed Treatment	1	0.00466	0.00466	0.16429	0.692
SoilxSeed Treatment	2	0.12635	0.06318	2.22722	0.150
Error	12	0.34038	0.02837		
Total	17	0.48450	0.02850		

Moderate Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.38054	0.19027	3.97023	0.047
Seed Treatment	1	0.00463	0.00463	0.09661	0.761
SoilxSeed Treatment	2	0.00658	0.00329	0.06865	0.934
Error	12	0.57509	0.04792		
Total	17	0.96684	0.05687		

High Wind Speed — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Soil	2	0.19732	0.09866	3.22559	0.076
Seed Treatment	1	0.28991	0.28991	9.47831	0.010
SoilxSeed Treatment	2	0.02233	0.01117	0.36503	0.702
Error	12	0.36704	0.03059		
Total	17	0.87660	0.05156		

APPENDIX B
ANOVA TABLES
MAIN GERMINATION STUDY
III WIND TUNNEL SOWN SEED VS CONTROL SEED

ANALYSIS OF CUMULATIVE GERMINATION PERCENT AT INDICATED TIME AFTER START OF GROWTH CHAMBER GERMINATION TEST

48 HOURS

Low Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.71491	0.10213	3.68198	0.012
Error	18	0.49928	0.02774		
Total	25	1.21419			

Moderate Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.83733	0.11962	2.90231	0.032
Error	18	0.74187	0.04122		
Total	25	1.57920			

High Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.93137	0.13305	19.74729	0.000
Error	18	0.12128	0.00674		
Total	25	1.05265			

72 HOURS

Low Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	1.10930	0.15847	8.46083	0.000
Error	18	0.33714	0.01873		
Total	25	1.44644			

Moderate Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.28887	0.04127	2.90171	0.032
Error	18	0.25599	0.01422		
Total	25	0.54486			

High Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	1.98203	0.28315	12.26955	0.000
Error	18	0.41539	0.02308		
Total	25	2.39742			

APPENDIX B continued

ANOVA TABLES
III WIND TUNNEL SOWN SEED VS CONTROL SEED

96 HOURS

Low Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.03997	0.00571	0.56312	0.776
Error	18	0.18252	0.01014		
Total	25	0.22249			

Moderate Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.70701	0.10100	3.47077	0.016
Error	18	0.52381	0.02910		
Total	25	1.23082			

High Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.55042	0.07863	4.22308	0.006
Error	18	0.33515	0.01862		
Total	25	0.88557			

168 HOURS

Low Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.15846	0.02264	1.08870	0.410
Error	18	0.37427	0.02079		
Total	25	0.53273			

Moderate Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.46610	0.06659	2.02525	0.108
Error	18	0.59180	0.03288		
Total	25	1.05790			

High Wind Speed

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Treatments	7	0.82783	0.11826	5.12731	0.002
Error	18	0.41517	0.02307		
Total	25	1.24300			

APPENDIX B

ANOVA TABLES
MAIN GERMINATION STUDY
IV COMPARISON BETWEEN CONTROLS

ANALYSIS OF CUMULATIVE GERMINATION PERCENT AT INDICATED TIME AFTER START OF GROWTH CHAMBER GERMINATION TEST

48 Hours — Transformation Used: None Required

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Seedlot/Time *	2	104.08083	52.04042	-	-
Restriction Error (∂)	0	0.00000		-	-
Seed Treatment	1	886.95041	886.95041	276.36831	0.000
Seedlot x Seed Treatment	2	104.08083	52.04042	16.21547	0.000
Error	18	57.76750	3.20931		
Total	23	1152.87957			

* Seedlot refers to seed prepared for each wind speed run.

72 Hours — Transformation Used: arcsin√germination percent

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Seedlot/Time	2	0.08769	0.04385	-	-
Restriction Error (∂)	0	0.00000		-	-
Seed Treatment	1	0.66197	0.66197	129.94730	0.000
Seedlot x Seed Treatment	2	0.08647	0.04324	8.48766	0.003
Error	18	0.09169	0.00509		
Total	23	0.92782			

96 Hours — Transformation Used: arcsin√germination percent

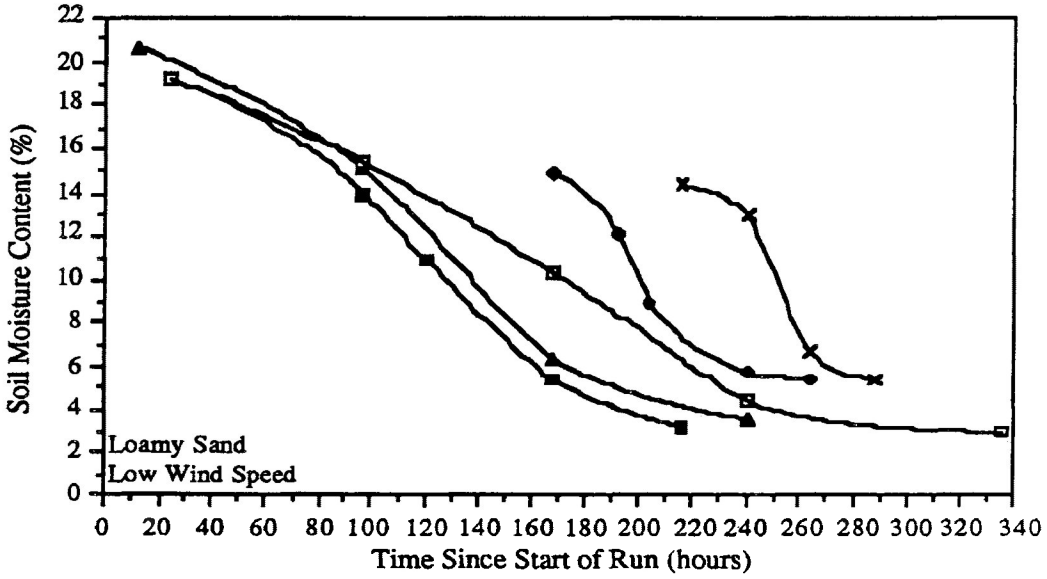
Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Seedlot/Time	2	0.29871	0.14936	-	-
Restriction Error (∂)	0	0.00000		-	-
Seed Treatment	1	0.02516	0.02516	3.05466	0.098
Seedlot x Seed Treatment	2	0.03816	0.01908	2.31666	0.127
Error	18	0.14824	0.00824		
Total	23	0.51027			

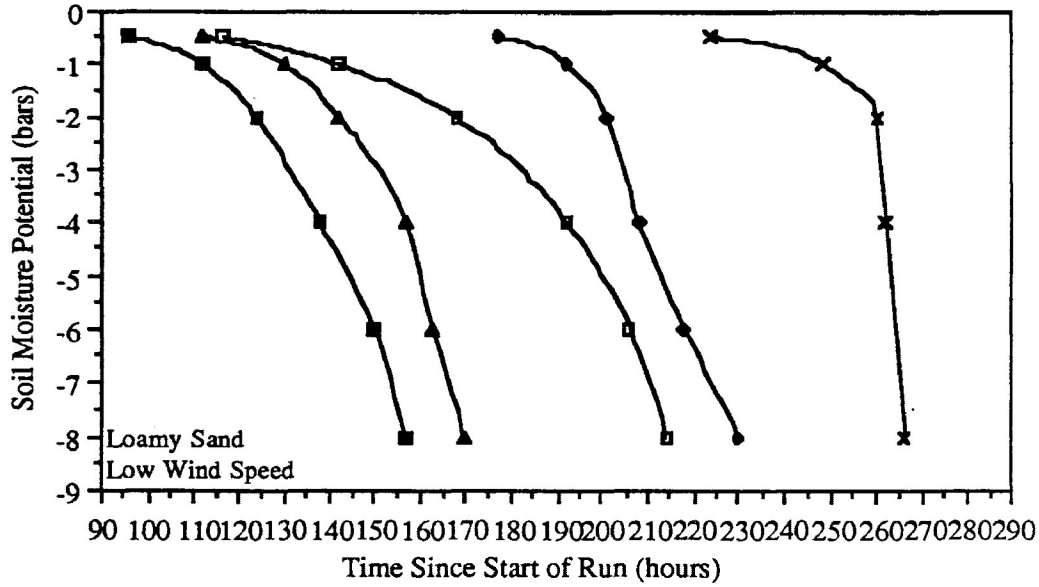
168 Hours — Transformation Used: None Required

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Seedlot/Time	2	24.75583	12.37792	-	-
Restriction Error (∂)	0	0.00000		-	-
Seed Treatment	1	6.00000	6.00000	1.56081	0.228
Seedlot x Seed Treatment	2	24.64750	12.32375	3.20583	0.064
Error	18	69.19503	3.84417		
Total	23	124.59836			

APPENDIX C

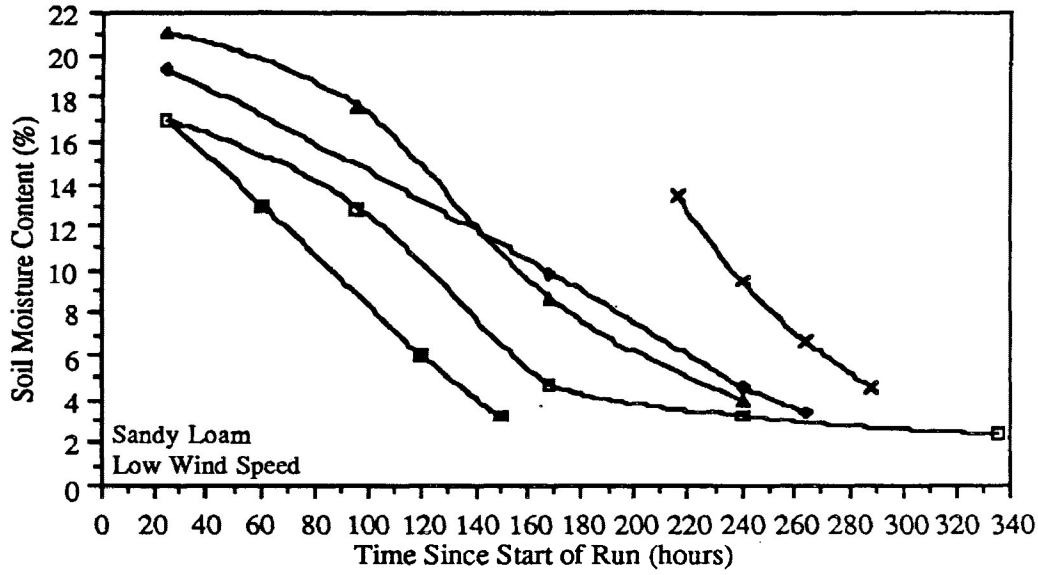
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (●), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□) STUDIES.

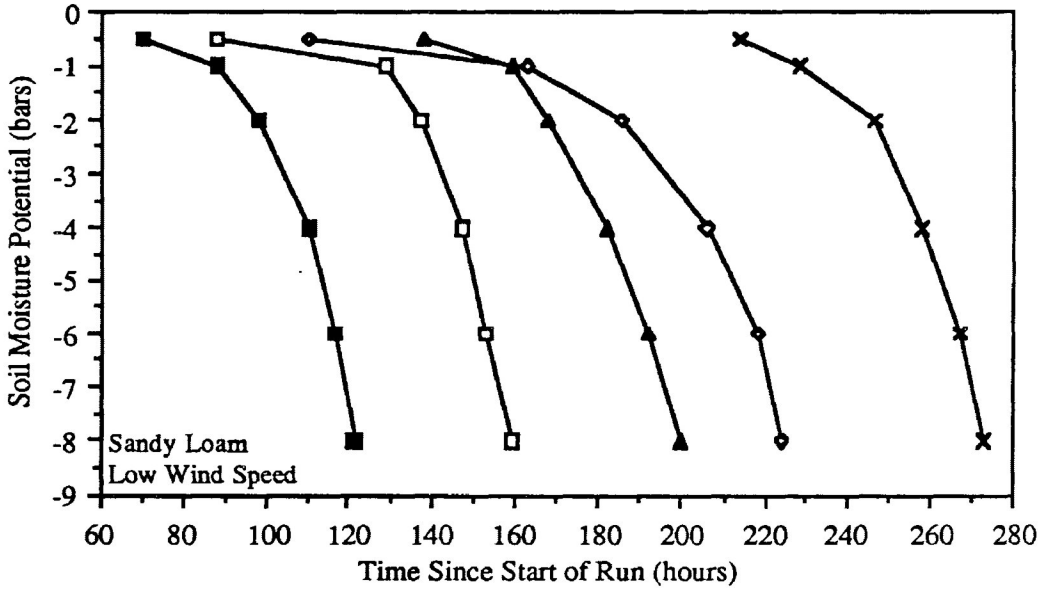




APPENDIX C- continued

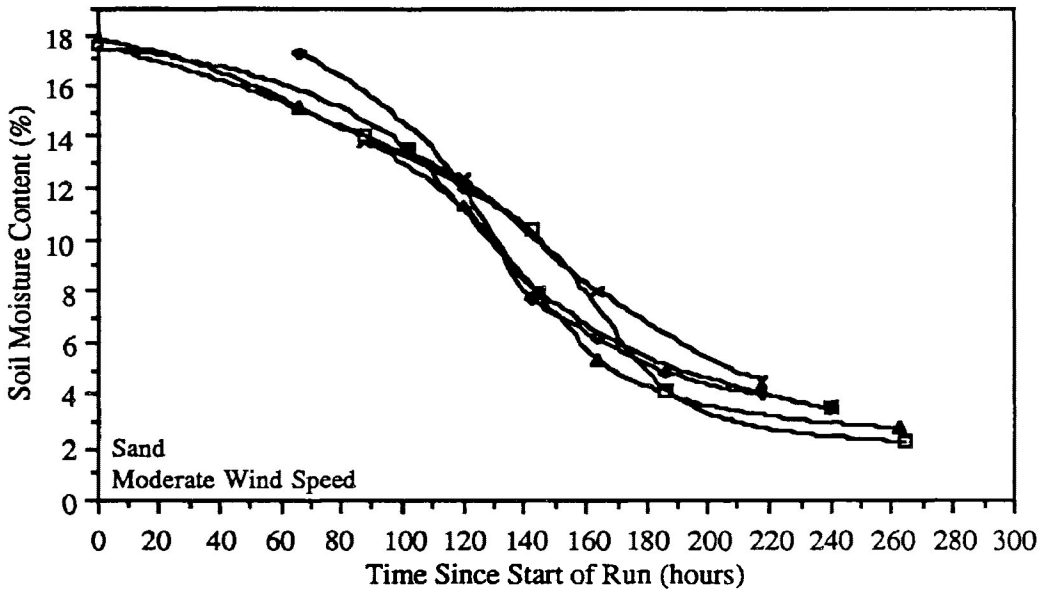
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (◆), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□) STUDIES.

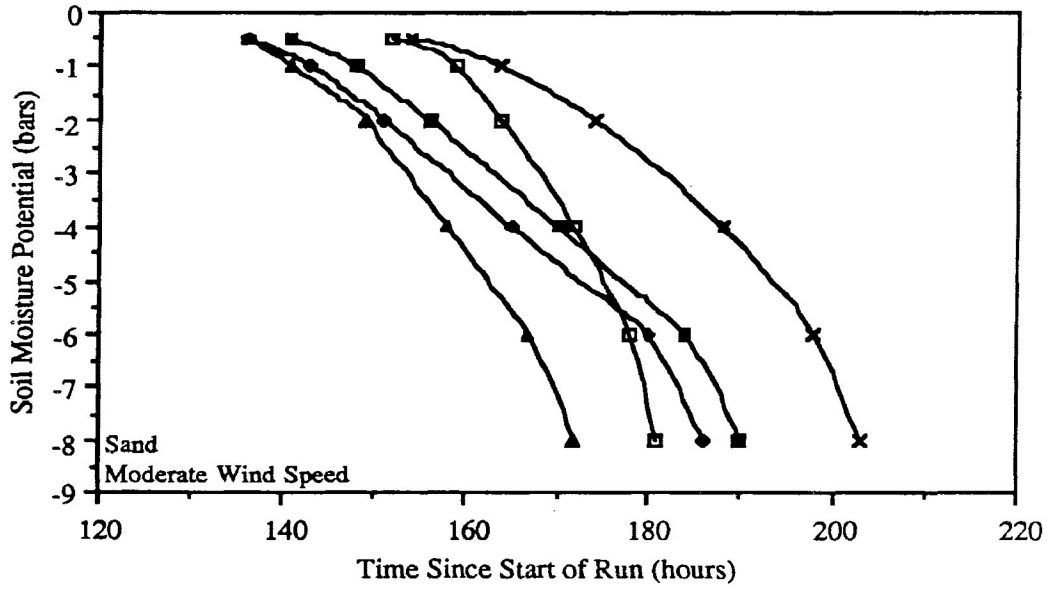




APPENDIX C- continued

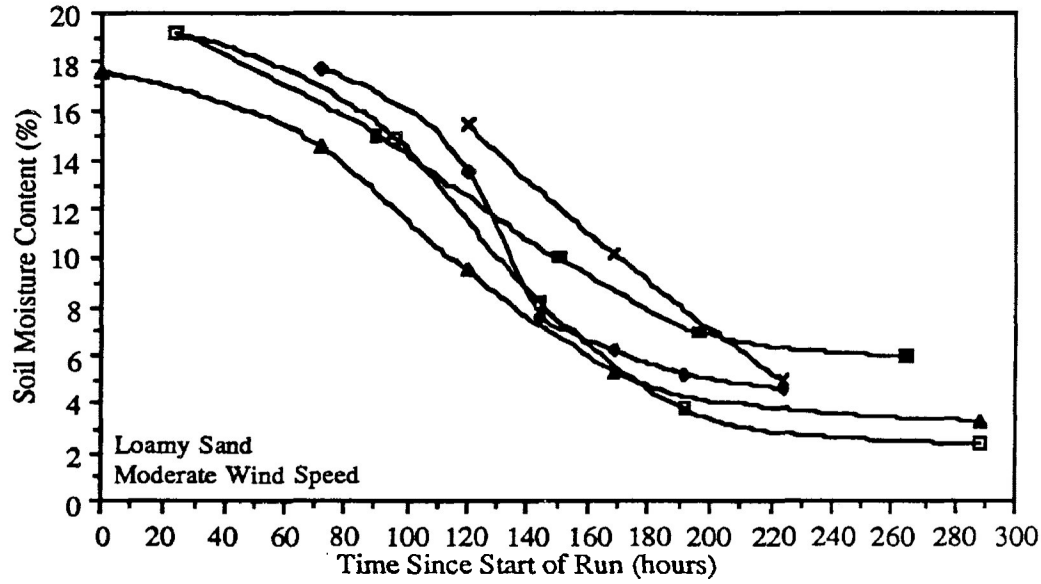
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (●), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□) STUDIES.

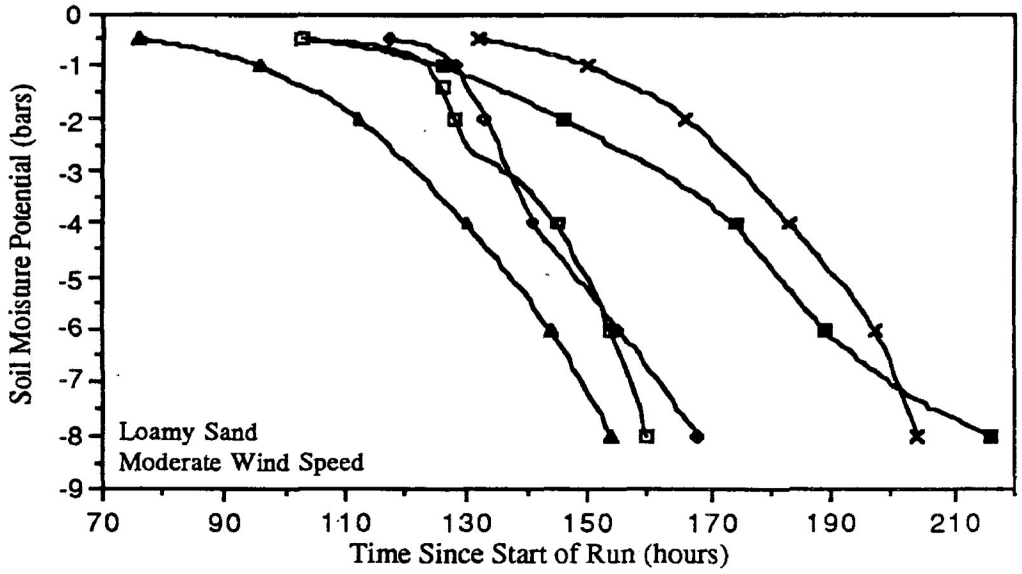




APPENDIX C- continued

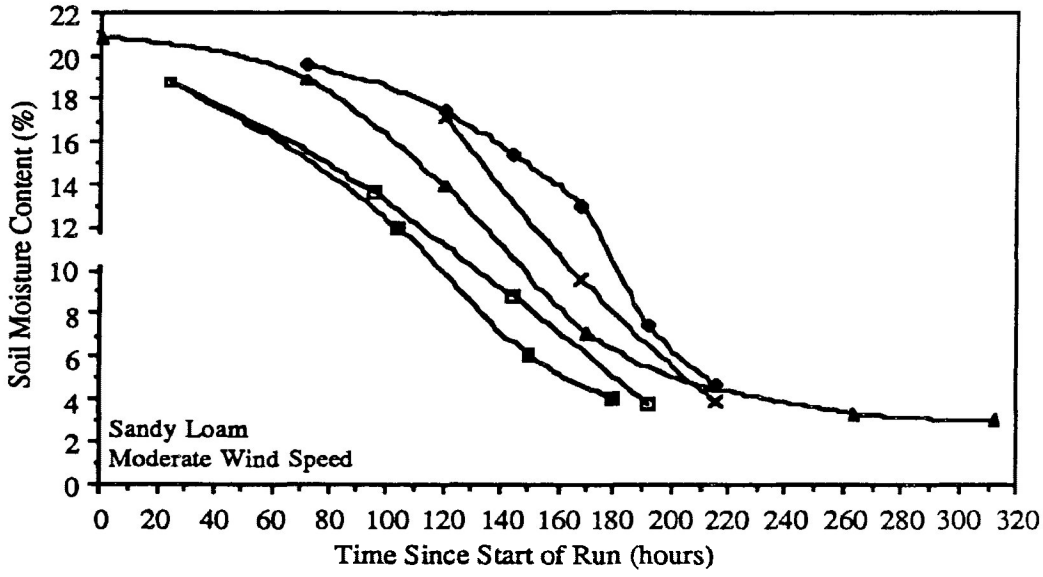
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (◆), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□)) STUDIES.

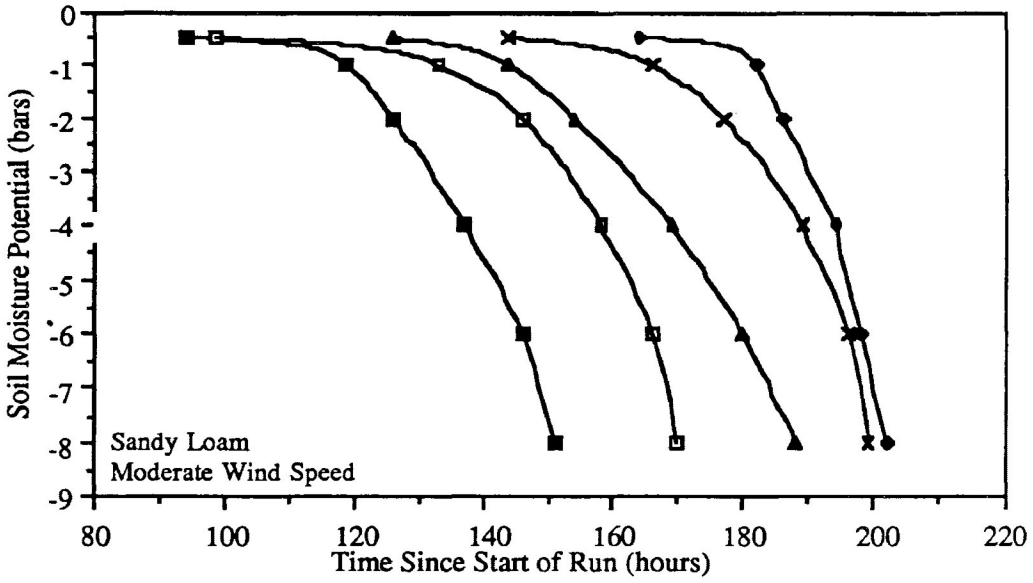




APPENDIX C- continued

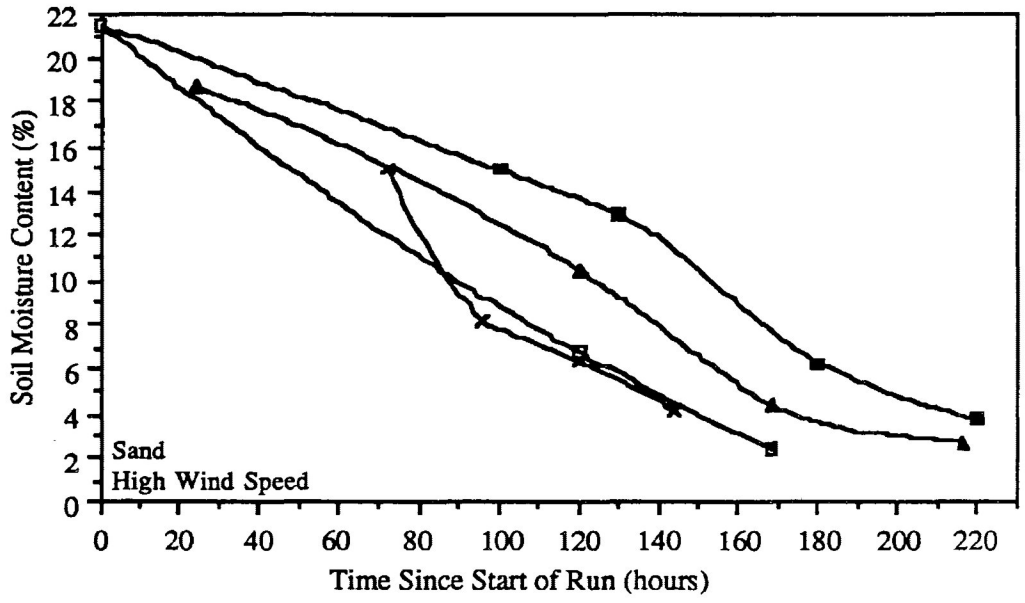
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (◆), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□)) STUDIES.

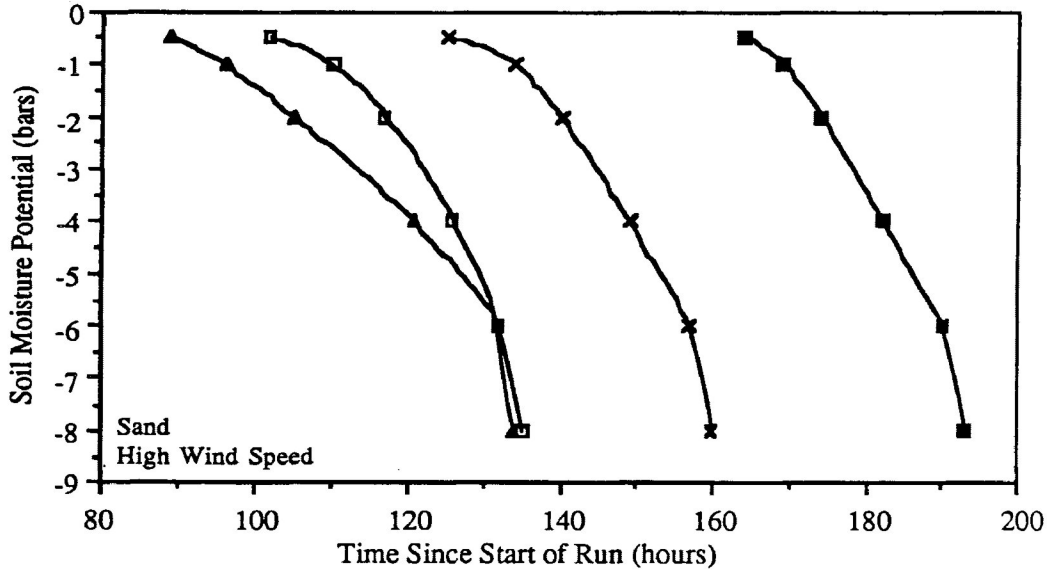




APPENDIX C- continued

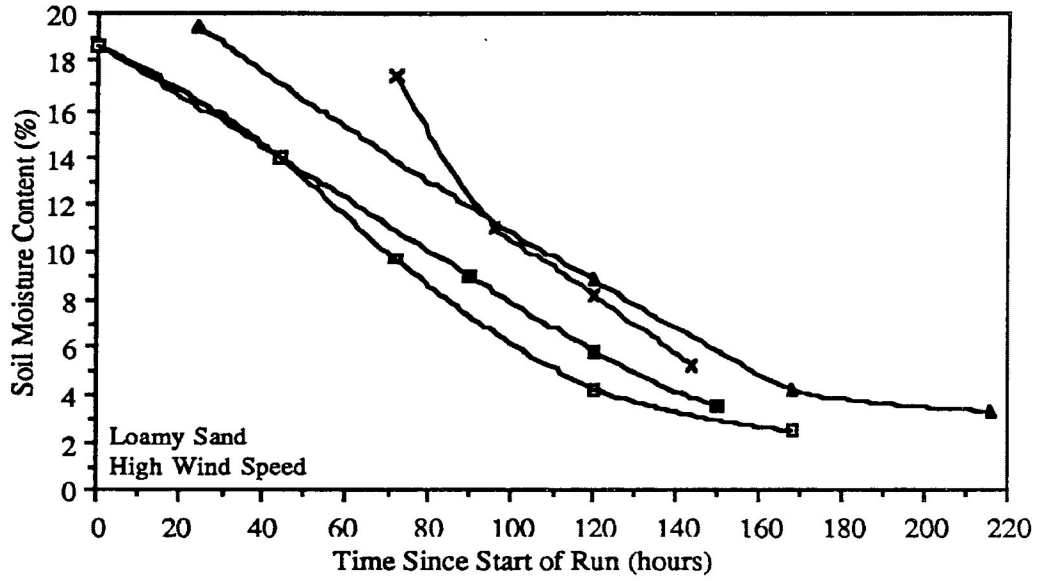
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (◆), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□)) STUDIES.

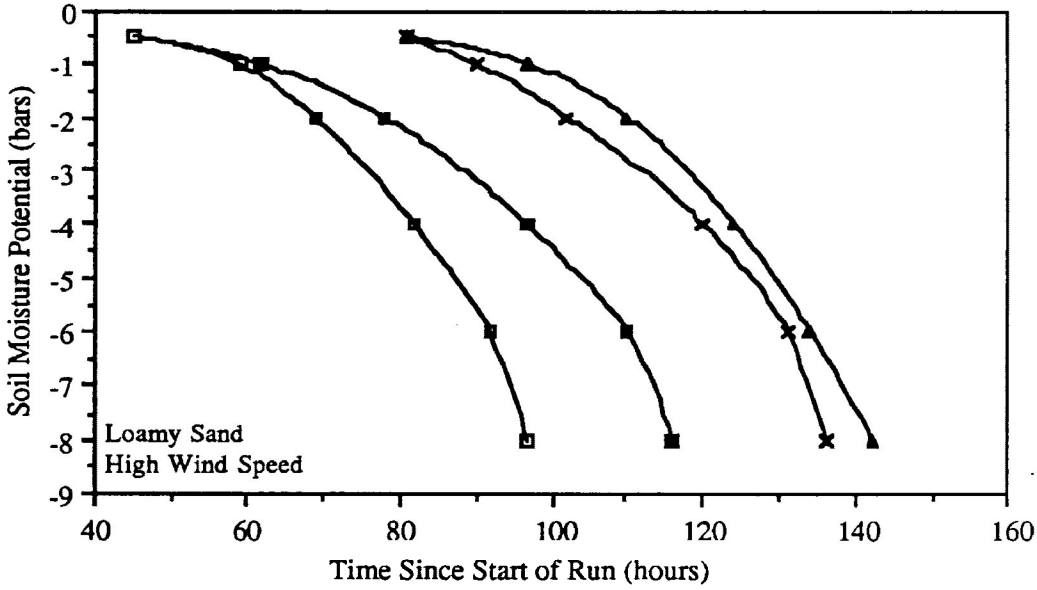




APPENDIX C- continued

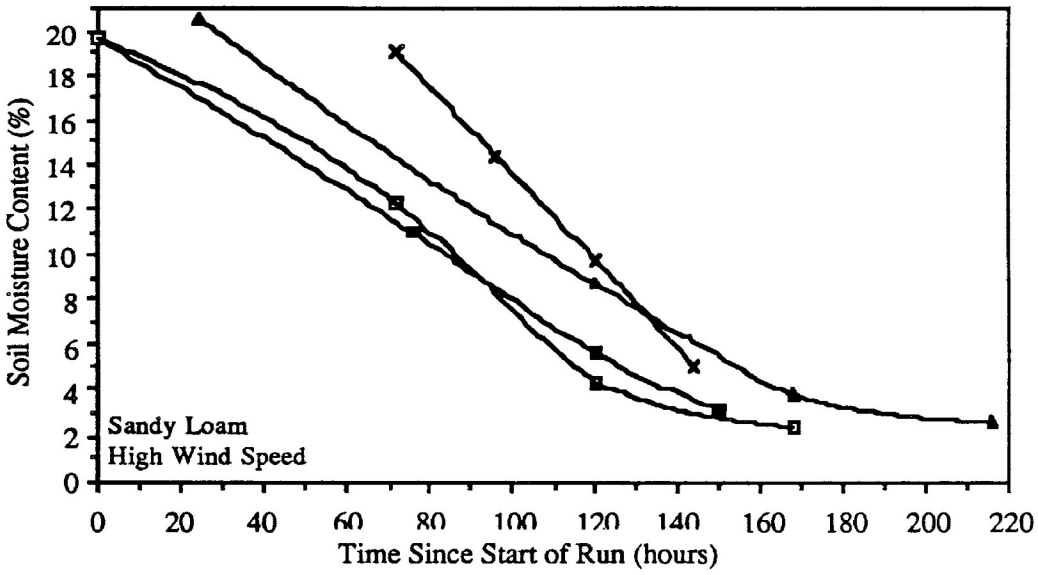
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (◆), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□)) STUDIES.

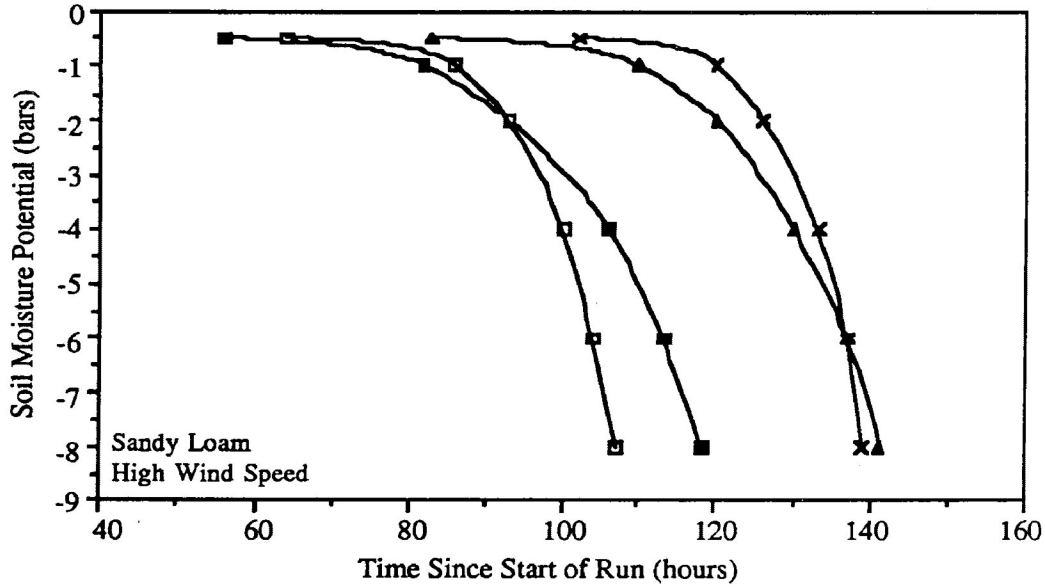




APPENDIX C- continued

SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL CURVES FOR THE SOIL DRYING (✖), PRELIMINARY GERMINATION (●), ONTOGENY (▲), AND MAIN GERMINATION (PROJECTED (■) AND ACTUAL (□)) STUDIES.





APPENDIX D

MEAN CUMULATIVE GERMINATION PERCENT OF WIND TUNNEL SOWN SEED AT THE INDICATED TIME AFTER THE START OF THE GROWTH CHAMBER GERMINATION TEST

24 HOURS

SEED TREATMENT	SOIL TYPE	WIND SPEED		
		Low	Moderate	High
Primed	Sand	2.4	2.2	0
	Loamy Sand	14	7.2	0
	Sandy Loam	0	0	0
Unprimed	Sand	11.1	0	2.2
	Loamy Sand	6.7	0	0
	Sandy Loam	6.7	2.2	2.2

48 HOURS

SEED TREATMENT	SOIL TYPE	WIND SPEED		
		Low	Moderate	High
Primed	Sand	11.6	16.6	15.2
	Loamy Sand	20.3	18.7	28.8
	Sandy Loam	22.6	19.2	11.2
Unprimed	Sand	18.2	2.4	10.9
	Loamy Sand	24.8	25.5	0
	Sandy Loam	16.4	4.4	1.0

72 HOURS

SEED TREATMENT	SOIL TYPE	WIND SPEED		
		Low	Moderate	High
Primed	Sand	74.4	44.8	67.7
	Loamy Sand	74.5	57.7	74.5
	Sandy Loam	80.4	45.3	60.1
Unprimed	Sand	59.3	26.8	17.7
	Loamy Sand	64.4	51.1	10.9
	Sandy Loam	46.5	32.0	24.4

96 HOURS

SEED TREATMENT	SOIL TYPE	WIND SPEED		
		Low	Moderate	High
Primed	Sand	88.1	72.5	88.4
	Loamy Sand	90.6	88.9	86.7
	Sandy Loam	88.6	71.1	77.6
Unprimed	Sand	80.1	47.7	79
	Loamy Sand	86.7	75.6	75.5
	Sandy Loam	88.9	57.8	68.9

APPENDIX D continued

MEAN CUMULATIVE GERMINATION PERCENT OF
WIND TUNNEL SOWN SEED AT THE INDICATED TIME
AFTER THE START OF THE GROWTH CHAMBER GERMINATION TEST

168 HOURS

SEED TREATMENT	SOIL TYPE	WIND SPEED		
		Low	Moderate	High
Primed	Sand	99	80	91
	Loamy Sand	95	98	98
	Sandy Loam	93	87	93
Unprimed	Sand	89	78	62
	Loamy Sand	93	99	90
	Sandy Loam	99	90	79

MEAN CUMULATIVE GERMINATION PERCENT OF CONTROLS
AFTER THE START OF THE GROWTH CHAMBER GERMINATION TEST

Time *	Seedlot ** (Wind Speed)					
	1 (Low)		2 (Moderate)		3 (High)	
	Seed Treatment					
	Primed	Unprimed	Primed	Unprimed	Primed	Unprimed
24	1.8	0	0.5	0	0.2	0
48	12.3	0	17.2	0	7.0	0
72	52.4	19.2	46.5	29.6	47.0	8.1
96	85.9	86.7	76.1	60.0	89.3	87.4
168	95.5	97.2	93.9	97.0	98.8	97.0

* Time after the start of the growth chamber germination tests.
** Seed primed in advance of each wind speed run in the wind tunnel.

APPENDIX E
RESULTS OF TUKEY'S TEST
WIND TUNNEL SOWN SEED VS CONTROL SEED

Soil Type/Control Seed Treatment		S[1] P[2]	S UP	SL P	SL UP	LS P	LS UP	C P	C UP
Time[4](hours)	Wind Speed	Mean Cumulative Germination Percent[3]							
48	Low	11.6ab	18.2b	22.6b	16.4ab	20.3b	24.8b	12.3ab	0.0a
48	Moderate	16.6ab	2.4ab	19.2ab	4.4ab	18.7ab	25.5a	17.2ab	0.0b
48	High	15.2bc	10.9b	11.2bc	0.0a	28.8c	1.0a	7.0b	0.0a
72	Low	74.4a	59.3a	80.4a	46.5ab	74.5a	64.4a	52.4a	19.2b
72	Moderate	44.8a	26.8a	45.3a	32.0a	57.7a	51.1a	46.5a	29.6a
72	High	67.7a	17.7cd	60.1ab	24.4bcd	74.5a	10.9d	47.0abc	8.1d
96	Low	88.1a	80.1a	88.6a	88.9a	90.6a	86.7a	85.9a	86.7a
96	Moderate	72.5ab	47.7b	71.1ab	57.8b	88.9a	75.6ab	76.1ab	60.0b
96	High	88.4a	79.0b	77.6ab	68.9ab	86.7a	75.5ab	89.3a	87.4a
168	Low	99.0a	89.0a	93.0a	99.0a	95.0a	93.0a	95.5a	97.2a
168	Moderate	80.0a	78.0a	87.0a	90.0a	98.0a	99.0a	93.9a	97.0a
168	High	91.0ab	62.0b	93.0ab	79.0ab	98.0a	90.0ab	98.8a	97.0a

[1] S- Sand, SL- Sandy Loam, LS- Loamy Sand, C- Control (Seed taken from cold storage.)

[2] P- Primed Seed, UP- Unprimed Seed

[3] Means having the same letter within a row are not significantly different at the 95 percent level of confidence.

[4] Time since the start of the growth chamber germination test.

APPENDIX F
ONTOGONY STUDY
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL AT TIME OF HARVEST- RAW DATA

Soil Type	Ontogeny Stage	Replication	Low Wind Speed		Mod Wind Speed		High Wind Speed	
			SMC	SMP	SMC	SMP	SMC*	SMP*
Sand	1	1	5.5	6.2	8.2	1.1	6.2	4.2
		2	4.7	15.0	6.0	4.7	6.0	4.7
		3	4.8	15.0	7.0	2.6	5.9	4.9
		4	3.0	<15.0	5.5	6.2	6.8	3.0
	2	1	4.0	<15.0	6.2	4.2	5.4	6.6
		2	5.2	8.0	5.6	5.9	5.7	5.5
		3	3.4	<15.0	6.4	3.7	5.6	5.9
		4	5.1	8.5	-	-	-	-
	3	1	4.3	<15.0	5.3	7.3	4.7	15.0
		2	4.2	<15.0	5.6	5.9	4.8	15.0
		3	4.8	15.0	-	-	4.7	15.0
		4	4.1	<15.0	-	-	5.1	8.6
	4	1	4.6	15.0	5.6	5.9	4.3	<15.0
		2	4.6	15.0	4.9	11.5	4.2	<15.0
		3	4.4	<15.0	5.7	5.5	-	-
		4	4.4	<15.0	5.7	5.5	-	-
	5	1	4.5	<15.0	5.0	9.5	4.0	<15.0
		2	4.4	<15.0	4.2	<15.0	4.0	<15.0
		3	4.6	<15.0	-	-	4.2	<15.0
		4	4.5	<15.0	-	-	3.8	<15.0
Loamy Sand	1	1	6.3	7.8	6.3	7.1	-	-
		2	6.3	7.8	6.8	6.2	-	-
		3	6.1	8.7	5.6	15.0	-	-
		4	6.0	9.3	8.4	3.6	-	-
	2	1	5.6	15.0	7.5	4.8	5.9	10.0
		2	5.5	15.0	7.0	5.7	6.8	6.2
		3	5.6	15.0	5.9	10.0	6.1	8.7
		4	5.3	<15.0	6.8	6.2	6.1	8.7
	3	1	5.4	<15.0	6.9	6.0	6.4	7.3
		2	5.4	<15.0	6.4	7.3	5.5	15.0
		3	5.5	15.0	6.7	6.0	5.7	15.0
		4	-	-	6.2	8.2	4.5	<15.0
	4	1	5.4	<15.0	6.4	7.3	6.3	7.8
		2	5.4	<15.0	6.6	6.7	5.2	<15.0
		3	5.3	<15.0	6.8	6.2	6.1	8.6
		4	5.3	<15.0	-	-	6.3	7.7
	5	1	5.3	<15.0	5.8	11.5	6.2	8.2
		2	5.3	<15.0	5.6	15.0	5.8	12.0
		3	5.5	<15.0	6.0	9.2	6.4	8.3
		4	5.3	<15.0	5.7	15.0	6.0	9.2

APPENDIX F
ONTOGONY STUDY
SOIL MOISTURE CONTENT AND SOIL MOISTURE POTENTIAL
AT TIME OF HARVEST- RAW DATA
continued

Soil Type	Ontogeny Stage	Replication	Low Wind Speed SMC	Low Wind Speed SMP	Mod Wind Speed SMC	Mod Wind Speed SMP	High Wind Speed SMC*	High Wind Speed SMP*
Sandy	1	1	5.8	8.5	5.5	11.4	-	-
Loam		2	6.0	7.5	5.5	11.4	-	-
		3	-	-	6.3	6.5	-	-
		4	-	-	5.7	9.0	-	-
	2	1	5.2	15.0	4.3	<15.0	5.3	15.0
		2	5.3	15.0	7.2	4.1	5.6	10.2
		3	5.4	15.0	5.7	9.0	5.6	10.2
		4	-	-	5.0	<15.0	-	-
	3	1	5.8	8.5	5.7	9.0	6.4	6.2
		2	5.9	8.0	5.1	<15.0	5.4	14.6
		3	5.8	8.5	6.0	7.6	7.4	5.0
		4	5.7	9.0	4.4	<15.0	-	-
	4	1	4.9	<15.0	5.6	10.0	6.9	4.7
		2	5.0	<15.0	4.8	<15.0	4.3	<15.0
		3	5.6	10.1	5.0	<15.0	4.0	<15.0
		4	5.7	9.0	5.5	11.4	6.5	5.8
	5	1	5.4	13.0	4.4	<15.0	5.7	9.1
		2	5.4	13.0	4.2	<15.0	5.6	10.0
		3	5.3	14.5	4.7	<15.0	6.4	6.1
		4	-	-	-	-	-	-

* SMC- Soil Moisture Content (%) SMP- Soil Moisture Potential (- bars)

APPENDIX G
LINEAR MODELS AND EXPECTED MEAN SQUARES TABLE
ONTOGENY STUDY

Linear Model

$$Y_{ijkl} = \mu + W_i + \partial + O_j + WO_{ij} + S_k + WS_{ik} + OS_{jk} + WOS_{ijk} + E_{(ijk)l}$$

where: μ is the grand mean
W is the i-th wind speed
∂ is the restriction error associated with running one wind speed at a time
O is the j-th ontogeny stage
S is the k-th soil type
E is the experimental error associated with the l-th replication of the jk-th treatment combination in the i-th wind speed

i= 1,2,3 Fixed Factor
j= 1,2,3,4,5 Fixed Factor
k= 1,2,3 Fixed Factor
l= 1,2,3,4 Random Factor

Expected Mean Squares Table

	3 F i	5 F j	3 F k	4 R l	
W_i	0	3	2	3	$Ó^2 + 60Ó^2(\partial) + 60Ø(W)$
$\partial(i)$	1	3	2	3	$Ó^2 + 60Ó^2(\partial)$ (restriction error)
O_j	3	0	2	3	$Ó^2 + 36Ø(O)$
WO_{ij}	0	0	2	3	$Ó^2 + 12Ø(WO)$
S_k	3	3	0	3	$Ó^2 + 60Ø(S)$
WS_{ik}	0	3	0	3	$Ó^2 + 20Ø(WS)$
OS_{jk}	3	0	0	3	$Ó^2 + 12Ø(OS)$
WOS_{ijk}	0	0	0	3	$Ó^2 + 4Ø(WOS)$
$E_{(ijk)l}$	1	1	1	1	$Ó^2$

APPENDIX H

ANOVA TABLES
ONTOGENY STUDY

Shoot Length Increment

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.2322	0.1161	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	0.0279	0.0139	26.2045	0.000
Ontogeny Stage.	4	5.3879	1.3470	2531.1279	0.000
Wind Speed x Soil Type	4	0.0497	0.0124	23.3529	0.000
Wind Speed x Ontogeny Stage	8	0.7875	0.0984	184.9726	0.000
Soil Type x Ontogeny Stage	8	0.2980	0.0373	69.9977	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	0.5052	0.0316	59.3301	0.000
Error	125	0.0665	0.0005		
Total	169	7.3549			

Shoot Length Value

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	1228.6404	614.3202	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	245.1437	122.5718	61.2798	0.000
Ontogeny Stage.	4	2037.9592	509.4898	254.7194	0.000
Wind Speed x Soil Type	4	361.2180	90.3045	45.1477	0.000
Wind Speed x Ontogeny Stage	8	543.3040	67.9130	33.9531	0.000
Soil Type x Ontogeny Stage	8	299.4952	37.4369	18.7166	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	468.8500	29.3031	14.6501	0.000
Error	125	250.0250	2.0002		
Total	169	5434.6355			

Root Length Increment

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	1.9161	0.9580	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	1.5233	0.7617	88.5777	0.000
Ontogeny Stage.	4	2.5903	0.6476	75.3095	0.000
Wind Speed x Soil Type	4	2.1013	0.5253	61.0946	0.000
Wind Speed x Ontogeny Stage	8	4.9320	0.6165	71.6960	0.000
Soil Type x Ontogeny Stage	8	1.6323	0.2040	23.7294	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	2.2468	0.1404	16.3306	0.000
Error	125	1.0748	0.0086		
Total	169	18.0169			

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Root Length Value

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	55.0354	27.5177	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	113.4284	56.7142	292.4873	0.000
Ontogeny Stage.	4	507.2977	126.8244	654.0604	0.000
Wind Speed x Soil Type	4	103.8722	25.9681	133.9228	0.000
Wind Speed x Ontogeny Stage	8	60.9633	7.6204	39.3001	0.000
Soil Type x Ontogeny Stage	8	10.9759	1.3720	7.0756	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	27.8250	1.7391	8.9687	0.000
Error	125	24.2379	0.1939		
Total	169	903.6358			

Root Dry Weight Increment

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	5.5461	2.7731	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	0.2984	0.1492	2.2531	0.112
Ontogeny Stage.	2	3.7289	1.8644	28.1513	0.000
Wind Speed x Soil Type	4	0.5581	0.1395	2.1067	0.088
Wind Speed x Ontogeny Stage	4	0.4394	0.1098	1.6586	0.168
Soil Type x Ontogeny Stage	4	0.2524	0.0631	0.9529	0.438
Wind Speed x Soil Type x Ontogeny Stage	8	0.2452	0.0306	0.4627	0.879
Error	76	5.0334	0.0662		
Total	102	16.1019			

Root Dry Weight Value

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.3163	0.1582	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	0.3435	0.1717	90.6387	0.000
Ontogeny Stage.	4	3.6959	0.9240	91.3696	0.000
Wind Speed x Soil Type	4	0.3133	0.0783	41.3372	0.000
Wind Speed x Ontogeny Stage	8	0.4860	0.0607	32.0615	0.000
Soil Type x Ontogeny Stage	8	0.1231	0.0154	8.1239	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	0.1618	0.0101	5.3372	0.000
Error	125	0.2368	0.0019		
Total	169	5.6768			

APPENDIX H- continued

ANOVA TABLES
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Shoot Dry Weight Increment

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.1147	0.0573	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	0.0052	0.0026	2.2292	0.114
Ontogeny Stage.	2	0.1457	0.0728	61.0692	0.000
Wind Speed x Soil Type	4	0.0047	0.0012	1.0237	0.400
Wind Speed x Ontogeny Stage	4	0.0278	0.0069	6.0145	0.000
Soil Type x Ontogeny Stage	4	0.0049	0.0012	1.0497	0.387
Wind Speed x Soil Type x Ontogeny Stage	8	0.0095	0.0012	1.0323	0.420
Error	76	0.0878	0.0012		
Total	102	0.4002			

Shoot Dry Weight Values

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	2.4223	1.2111	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	2.7875	1.3937	98.9100	0.000
Ontogeny Stage.	4	44.5960	11.1490	259.5582	0.000
Wind Speed x Soil Type	4	2.1934	0.5483	38.9144	0.000
Wind Speed x Ontogeny Stage	8	3.2503	0.4063	28.8331	0.000
Soil Type x Ontogeny Stage	8	0.5460	0.0683	4.8439	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	0.6873	0.0430	3.0483	0.000
Error	125	1.7614	0.0141		
Total	169	58.2441			

Total Dry Weight Increment

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	0.0342	0.0171	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	0.0248	0.0124	13.8773	0.000
Ontogeny Stage.	4	1.0491	0.2623	423.8788	0.000
Wind Speed x Soil Type	4	0.0118	0.0030	3.3014	0.013
Wind Speed x Ontogeny Stage	8	0.0811	0.0101	11.3480	0.000
Soil Type x Ontogeny Stage	8	0.0136	0.0017	1.9025	0.065
Wind Speed x Soil Type x Ontogeny Stage	16	0.0099	0.0006	0.6925	0.794
Error	124	0.1108	0.0009		
Total	168	1.3353			

APPENDIX H- continued

ANOVA TABLES
ONTOGENY STUDY

Total Dry Weight Value

Source of Variation	df	Sum of Squares	Mean Square	F	Significance of F
Wind Speed/Time	2	3.3159	1.6579	-	-
Restriction Error (∂)	0	0.0000		-	-
Soil Type	2	3.9810	1.9905	111.7636	0.000
Ontogeny Stage.	4	50.9632	12.7408	182.6409	0.000
Wind Speed x Soil Type	4	3.0166	0.7541	42.3438	0.000
Wind Speed x Ontogeny Stage	8	4.5555	0.5694	31.9731	0.000
Soil Type x Ontogeny Stage	8	0.7906	0.0988	5.5491	0.000
Wind Speed x Soil Type x Ontogeny Stage	16	1.1161	0.0698	3.9168	0.000
Error	124	2.2084	0.0178		
Total	168	69.9473			