STUDIES ON WATERLOGGING TOLERANCE IN LUCERNE, *Medicago sativa*, L.

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by

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SUMMARY

The tolerance to waterlogging of eight lucerne varieties was assessed in the glasshouse using three South Australian soils which are prone to waterlogging during the winter. Four introduced varieties from Russia and North America, which have a common ancestry in the floodland ecotypes of central European Russia, were more tolerant than four Australian registered varieties. Under flooding the introduced varieties were higher yielding and retained a higher proportion of actively growing plants. The effect of flooding varied between the three soils, but the ranking of the response of the varieties was generally similar in all the soils.

In a second glasshouse experiment hybrid populations of crosses between the four tolerant varieties and the four Australian varieties were intermediate in performance when assessed for yield, shoot production, retention of meristemmatic activity and a score for leaf colour, senescence and loss. The population x soil interactions within the flooded treatment were again generally insignificant.

A group of four parents, two tolerant and two intolerant under glasshouse conditions, and hybrids between these tolerant and intolerant parents were studied as replicated clones of individual plants in a flooded field experiment conduced during the winter at Meadows, near Adelaide. Survivors from the previous experiment and unselected control clones were included. There were few significant differences between the survivors and the control population when they were compared by measuring components of plant growth and assessing their appearance.

In the field the tolerant introduced parents were more winter-dormant than the intolerant Australian varieties and for a number of weeks after flooding was imposed they suffered less deterioration of their leaf tissue and the hybrid populations once again were intermediate.

After prolonged flooding almost all the surviving clones were hybrids and all the parental clones, except for a small number of one introduced variety, had been killed.

The most consistent criteria for assessing the tolerance of populations and clones in either the glasshouse or field were the retention of meristemmatic activity and the appearance of leaf tissue. Plant yield was not a reliable criterion for selection in the glasshouse because the prevailing temperature and light conditions did not permit resolution of differences in winter-dormancy. Regrowth after flooding in the glasshouse was not a suitable index for the selection of tolerant plants. Shoot production per plant under both flooded and nonflooded conditions reflected varietal differences in the propensity to produce shoots and plant dormancy rather than flooding tolerance.

The methods which might be used to continue selection for a lucerne population incorporating both waterlogging tolerance and other desirable agronomic characteristics are discussed. The intravarietal variation expressed by the four introduced varieties and one Australian variety, 'Demnat', and the superior performance after prolonged flooding of some individual clones from first generation hybrids indicate that the breeding of a waterlogging tolerant variety adapted to southern Australia can be pursued.

TABLE OF CONTENTS

TABLE OF CONTENTS (Contd.)

TABLE OF CONTENTS (Contd.)

TABLE OF CONTENTS (Contd.)

TABLE OF CONTENTS (Contd.)

TABLE OF CONTENTS (Contd.)

STATEMENT

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

IAN D. KAEHNE
APRIL, 1976.

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1. INTRODUCTION

Lucerne (*Medicago sativa*, L.) is a major fodder and pasture species in Australia used extensively in a broad arc sweeping from the mid-northern agricultural areas of South Australia to south-eastern Queensland. It has a major concentration of production in western and southern New South Wales and the south-east of South Australia.

The overwhelmingly dominant variety is 'Hunter River', which originated on the flats of the Hunter River, New South Wales early in the nineteenth century from introduced lucerne of unknown, but possibly European, origin. The three major factors in the adaptation of this variety are the hydrology of the site, the pH of the soil and the presence of virulent pathogens.

In extensive areas of southern and eastern Australia (in Western Australia, South Australia, Victoria, Tasmania, New South Wales and Queensland) duplex soils occur. These have a permeable surface horizon of variable depth overlying a relatively impermeable horizon or have a natural watertable close to the soil surface. During winter and spring, which are the seasons of maximum precipitation and minimum evaporation, these soils are susceptable to waterlogging of the surface horizon for periods of up to three or four months.

'Hunter River' and other lucerne varieties presently cultivated in Australia are damaged by waterlogged conditions that persist for more than two or three weeks so lucerne is only sown on those areas of duplex soils which are not susceptible to prolonged waterlogging.

Because existing Australian varieties of lucerne are severely restricted by the conditions under which they can persist, the legume component of pastures and fodder crops on the waterlogged soils is provided by other perennial and annual legume species. The principle species employed are *Trifolium fragiferum* (Strawberry clover), *Trifolium repens* (white clover) and *Trifolium subterraneum* subsp. vanninicum(Subterranean clover).

Although these species are more tolerant to waterlogging they do not have some of the other desirable agronomic characteristics of lucerne, particularly the adaptation of lucerne to hot dry summer conditions, its perenniality and suitability for modern haymaking and fodder harvesting. Therefore, this study is concerned with the expression of waterlogging tolerance in introduced lucerne varieties and hybrids between these and local varieties.

Four varieties of lucerne cultivated in the Soviet Union, Canada and U.S.A. have been reported to be tolerant to waterlogged, poorly drained and acid soils. They all have as a common ancestor a wild species, Medicago falcata, which occurs in the floodlands of the rivers of central European Russia.

The experiments reported compare the growth of these four varieties with four Australian varieties. The first experiment compared the growth of the eight varieties under flooded and unflooded conditions in pots in three soils in the glasshouse. The fresh and dry weight of plant tops and roots and the appearance of plants were recorded at four harvests during forty days of flooding.

In a second experiment the tolerance to flooding of the hybrids between these eight varieties was compared with the eight parents. The yield of plant tops, the number of shoots and the visual appearance of plants were used to measure the effect of flooding for five weeks on two month old seedlings. Subsequent recovery from flooding was determined by plant top yield, the number of shoots and proportion of surviving plants after six weeks regrowth. The experiment was conducted in a glasshouse in the same three soils used in the first experiment.

From plants surviving after flooding in Experiment 2, clones were selected from the crosses between two tolerant types and two Australian cultivars. Unselected clones were also taken from the nonflooded treatment.

These clones were propagated and planted in the field near Meadows in the Adelaide Hills where they were subjected to flooding for thirteen weeks. The yield, height, shoot number and shoot length were obtained for each clone before and after flooding. During the period of flooding the clones were also visually rated for the effect of flooding.

These experiments provide a guide to the value of introduced lucerne varieties as a source of waterlogging tolerance in breeding a well-adapted waterlogging tolerant cultivar.

2. LITERATURE REVIEW

2.1. INTRODUCTION

Waterlogging of a soil can be regarded as that state which exists when the water content of the soil exceeds "field capacity". Depending upon the water content and the distribution of particle size in a soil this may result in either a three phase soil-water-air system containing more water than a freely drained soil at field capacity or a two-phase soil-water system. It is in this latter system that the narrower and more precise definition of waterlogging becomes "the state which occurs when water fills sufficient air spaces in a soil for a long enough period to restrict the diffusive interchange of the soil and above ground atmospheres to such an extent that the normal oxidative processes in a soil, chemical and biological, are inhibited." (Rowe, 1973)

The occurrence and longevity of waterlogging in a particular area place restraints upon the system of agricultural production which can be pursued in that area, the genotypes which are adapted to that area and their management for successful culture. This review will encompass the major effects of waterlogging on soils and plants and the adaptation and response of plants, particularly agriculturally important species, to waterlogged conditions. The review extends beyond the narrow field of the experimental portion of this thesis, namely genotypic differences under waterlogging in lucerne, because the specific literature on that topic is restricted to a few papers describing the agronomic effects. An understanding of the effects of waterlogging upon plants and the physiology of their response and adaptation must be drawn from other work to indicate possible mechanisms for differences in waterlogging tolerance in lucerne.

2.2. THE EFFECT OF WATERLOGGING ON THE PHYSICAL AND CHEMICAL STATE OF SOILS

In recent years the effect of waterlogging on the physical and chemical properties of soils and the interaction between these properties has been reviewed by a number of authors (Ponnamperuma, 1964, 1972; Rowe, 1973; Russell, 1973; van't Woudt and Hagan, 1957; Patrick and Mahapatra, 1968; Grable, 1966).

2.2.1. The effect of waterlogging on the concentration of oxygen in the soil

The primary physical effect of flooding is to displace air from the soil pores, which in a well aerated soil at field capacity may be 10 to 30 percent of the total volume (Grable, 1966). The water has the primary effect of reducing the diffusion rate of oxygen in the soil by a factor of approximately 10,000, being the comparative rate of oxygen diffusion in air and water respectively (Grable, 1966). The water which floods the soil may be saturated initially with oxygen from the air to a level of approximately 8×10^{-6} g. cm^{-3} (Letey and Stolzy, 1967), but the oxidation demand of the soil quickly depletes this oxygen and creates an anoxic state. In closed systems, Turner and Patrick (1968) recorded depletion of oxygen from four flooded soils within 18 to 36 hours, and Evans and Scott (1955) reported a decline to 1% of the original oxygen concentration after 75 minutes. In systems which are open to the atmosphere two zones are rapidly established in the soil, an oxidated surface layer and a reduced layer beneath. (Patrick and Mahapatra 1968). Greenwood and Goodman (1967) measured the oxygen concentration at various depths within saturated soil moulded into small spheres and reported a decline from 6×10^{-3} $ml_{O_2} ml^{-1} H_2O$ (the concentration in air saturated water) to zero within a distance of 2 mm from the surface, and within a partially drained column of soil crumbs, the gaseous oxygen concentration fell sharply from 10% to zero over a mean distance of 0.24 cm. In a rice field, Patrick and Sturgis (1955) recorded a decline in oxygen concentration in the soil from 8.2 p.p.m. at the soil surface to 0.3 p.p.m. at a depth of 6 cms with the sharpest decline between 5 and 6 cms. This soil had an oxygen demand of 1.2 p.p.m. hr^{-1} before flooding and 6.8 p.p.m. hr^{-1} after flooding demonstrating the potential for flooded soils to extract oxygen from the soil water.

The thin oxygenated surface layer is maintained by diffusion of oxygen from either the atmosphere or saturated flooding water into the soil. Williamson (1964) and Williamson and Schilfgaarde (1965) recorded oxygen diffusion rates (ODR) of approximately 2 to 3 x 10^{-8} gm cm^{-2} min^{-1} at a watertable and Poel (1960a) recorded 4.8 and 8.7 x 10^{-8} gm cm^{-2} min^{-1} as the ODR in a waterlogged site and the bed of a stream respectively.

In a soil with the watertable below the soil surface, capilliary action creates a zone above the free water level of reduced porosity, resulting in a decline in oxygen concentration as the watertable is approached. The partial pressure of oxygen fell from 130mm Hg at approximately 25cm to less than 30 mm Hg at 10 cm above the watertable in a fine sandy loam (Williamson and Schilfgaarde, 1965). (156 mm Hg is equivalent to the atmospheric oxygen concentration). The oxygen concentration was less than 7% in soil air less than 20cm above a watertable in the study by Kristensen and Enoch (1964).

2.2.2. The effect of waterlogging on the oxidation-reduction potential in soil

The electrochemical property which differentiates a submerged soil from a well aerated soil is its redox potential. Low potentials (0.2 to 0.4 volts) indicate the reduced state of waterlogged soils and high potentials (0.8 to 0.3 volts) the oxidized state of aerated media (Ponnamperuma, 1972).

In a paddy field Nishigaki et al., (1962) reported a decline from 0.31 volts at 1 cm depth to 0.25 volts at 3 to 5 cm depth and 0.1 volts below 8 cm, and De Gee (1950) reported a decline from 0.6 volts at the surface to 0.1 volts at 2 cm depth and .04 volts at 8 cm whereas an aerated profile maintained 0.6 to 0.7 volts throughout the profile.

Mortimer (1941) recorded a declining redox potential with depth in mud under aerated water with the limit of ferric ion stability being at 1 to 2 cm depth. The aerated water had a potential of approximately 0.5 volts. An anaerobic container reduced the redox potential at the mud surface from 0.48 volts to 0.06 volts in 140 days thereby demonstrating the effect of aerated water to maintain oxidated conditions in the surface of waterlogged soils.

Pearsall (1938) and Pierce (1953) correlated the distribution of natural vegetation in swamps and woodlands with redox potential. Pierce noted that the distribution of vegetation was also related to oxygen deficiency and specific conductance in the soil.

The decline in redox potential in soils can be related to a stepwise reduction in the number of inorganic ions in the soil, thereby changing the ionic conditions within the soil solution. (Ponnamperuma, 1964, 1972; Patrick and Mahapatra, 1968; Russell, 1973). When a soil is flooded the oxygen is depleted by aerobic respiration and the potential at the point of oxygen depletion is between 0.3 and 0.35 volts. Before this potential was reached, nitrate-N reduction to nitrite-N was commenced but the nitrite-N did not disappear before molecular oxygen. (Turner and Patrick, 1968). In soil suspensions of a silty loam with pH 5.1, Patrick (1960) concluded NO_3-N became unstable at 330 mV (equivalent to 224 mV at pH 7.0) and disappeared below and accumulated above that voltage.

Manganese reduction to soluble Mn^{++} ions was increased markedly below 200mV in the study of Turner and Patrick (1968), but reduction commenced soon after waterlogging commenced and did not appear to be retarded by the presence of NO_3-N. The transition of Mn from reducible to exchangeable forms was greatest over the range +400 to +300mV and was essentially complete at +200mV (Patrick and Turner, 1968). At lower redox values (+200mV to -100mV) Fe^{+++} iron is reduced to Fe^{++} iron and the availability of native and applied phosphorus is increased (Patrick, 1964; Savant and

Ellis, 1964). At extremely low potentials (-200mV) SO_4-S is reduced to sulphide -S and precipitation of FeS occurs if free Fe^{++} ions are available. (Armstrong, 1967d; Connell and Patrick, 1969).

2.2.3. The effect of waterlogging on the pH of soil

When an aerobic soil is submerged its pH may decrease during the first few days (Ponnamperuma, 1965; Bell, 1969) reach a minimum and then approach neutral within a few weeks. Bell (1969) concluded that the initial decline in pH is caused by the removal of oxygen and NO_3-N through microbial action releasing carbon dioxide, hydrogen and acidic organic products.

Mahapatra (1968) reported a decline in the range of pH of twenty soils from initial extreme values of pH 4.7 - 8.2 to pH 6.4 - 7.7 with most soils being near neutral after 60 days of flooding. Ponnamperuma (1972) summarizes possible chemical mechanisms for the kinetic trend of pH in submerged soils to approach values near neutral.

The pH in a waterlogged soil and the redox potential interact to influence the concentration of soluble ions in the soil solution. Turner and Patrick (1968) recorded high concentrations of exchangeable Mn in waterlogged soils with pH values less then 7 (approx 350 p.p.m. Mn) and a declining concentration as the pH rose to 8 (180 p.p.m. Mn) and virtual elimination at pH 11 (20 p.p.m. Mn). The levels in aerated soil were negligible. Gotah and Patrick (1974) described the interaction of pH, redox potential and concentration of Fe^{++} ions in a sandy loam and recorded a decrease in concentration at a fixed potential as the pH increased.

2.2.4. The effect of waterlogging on the specific conductance in the soil solution.

On flooding, most soils show a rise in specific conductance particularly after anoxic conditions are established (Mortimer, 1941;

Ponnamperuma, 1964) and after some weeks a peak conductance is reached and then a slow decline may occur (Ponnamperuma, 1972).

2.2.5. Changes in the concentration of nutrient ions and other elements in the soil as a result of waterlogging

2.2.5.1. Nitrogen

The major processes involving nitrogen in submerged soils are mineralization, denitrification and ammonia volatilization. Patrick and Mahapatra (1968), Ponnamparuma (1972) and Patrick and Wyatt (1964) recorded higher rates of mineralization under waterlogged than under aerobic conditions. Organic matter was mineralized and formed ammonium ions up to concentrations of 190 p.p.m.

Greenland (1962), Bremner and Shaw (1958) and Nommik (1956) reported studies on denitrification in soils. Denitrification is very slow at low pH values and reaches a peak at approximately pH 8.0. Increasing temperature and the content of readily oxidizable organic matter increased the rate of denitrification. Below moisture contents of 60 to 70% of field capacity no denitrification occurred, and continuous aeration of soil suspensions markedly reduced NO_3-N loss. In saturated soils having low oxygen concentrations the rate of denitrification is generally independent of the nitrate concentration. Patrick and Sturgis (1955) noted a decrease in NO_3-N during 30 days submergence of a rice soil, but the concentration of NH_3-N remained constant. Mortimer (1942) reported the reduction of nitrate to ammonium ions in lakes under anoxic conditions and Brandt, Wolcot and Erickson (1964) found NO_3-N hardly detectable in a saturated soil, with NH_4-N being the main form of nitrogen present.

The ammonia formed by denitrification togetherwith elemental nitrogen and nitrous oxide (N_2O) may be lost in gaseous form or alternatively leached down in the profile. (Ponnamperuma, 1972).

Bell (1969) concluded that the process of denitrification was correlated with a stable phase in redox potential at +200mV until all NO_3-N was eliminated, after which the potential continued to fall.

Yoshida, Takai and del Rosario (1975) measured the elemental nitrogen content below the soil surface in a rice field and concluded that rice plants were supplying gaseous nitrogen by internal diffusion to the rhizosphere and N- fixing bacteria.

2.2.5.2. Phosphorus

The review of Patrick and Mahapatra (1968) also discussed the effect of waterlogging on the availability of soluble phosphate. Islam and Elahi (1954) and Patrick (1964) suggest that the increase in phosphate solubility may be related to the reduction of ferric oxide in phosphatic co-precipitates to ferrous ions thus releasing phosphate. Other mechanisms are discussed in the above review. Savant and Ellis (1964) recorded a greater increase of available phosphate under declining redox potentials at lower pH values, and Mahapatra (1968) noted a general increase in a wide range of soils.

2.2.5.3. Manganese

The reduction of Mn^{+4} in insoluble compounds to soluble Mn^{+2} ions occurs quickly upon saturation and depletion of oxygen in soil and high concentrations are attained. (Graven, Attoe and Smith, 1965; Turner and Patrick 1968; Mandal, 1961). In acidic soil conditions the water soluble component of the reduced manganese is greater and is formed readily upon flooding (Gotoh and Patrick, 1972). They suggest that manganese reduction in flooded soil may not be solely determined by thermodynamic considerations, but are also regulated by microbiological oxidation-reduction processes and chelation by organic compounds.

2.2.5.4. Iron

The reduction of Fe^{+3} to Fe^{+2} occurs in waterlogged soils. (Mandal, 1961; Gotoh and Patrick, 1974; Turner and Patrick, 1961), but the effect may be slight (Mahapatra, 1968) and generally the reduction does not occur until NO_3-N is depleted from the soil. Rowe (1973) suggests this reduction is a buffering action against falling redox potential.

2.2.5.5. Other Elements

Under extreme conditions of low redox potential reduction of sulphate to sulphide may occur (Ponnamperuma, 1964), and Ng and Bloomfield (1962) concluded that flooding increased the availability of some heavy metals.

2.2.6. The metabolism of carbon in waterlogged soils

Respiration in soils may proceed at varying rates and carbon dioxide production may fall quite markedly in cool seasons or in soils approaching waterlogged conditions (Currie, 1975). The change from aerobic to anaerobic metabolism of organic materials takes place in widely differing soils when oxygen concentration becomes less than about 3×10^{-6}M (Greenwood, 1961).

Under anoxic conditions alternate electron acceptors such as manganic oxides, ferric compounds, nitrate and in extreme conditions sulphate and phosphate facilitate the respiration of anaerobes which utilize organic compounds as substates, resulting in the production of simple organic acids, simple alcohols, carbon dioxide, hydrogen and methane. (Ponnamperuma, 1964, 1972; Bell, 1969; Parr, 1969). The presence of readily oxidizable organic compounds (glucose, green manure) accelerates the chemical and physical changes which result from waterlogging a soil. (Bell, 1969).

2.2.7. The production of phytotoxic compounds in waterlogged soils

2.2.7.1. Nitrite and Nitrous Oxide

Nitrite is toxic to barley, bean and tomato at concentrations greater than 50 p.p.m. but effects are detectable at lower concentrations (Bingham, Chapman and Pugh, 1954). The tolerance depends upon the species, pH and form of nitrogen assimilated by the species. In a study of soil nitrate levels, Dowdell and Smith (1974) detected nitrite levels up to 4.5 mgm l^{-1} at 30 cm depth in a waterlogged clay soil. The relationship of oxygen and nitrous oxide was variable but high nitrous oxide concentrations were associated with oxygen concentrations less than 8 per cent, anaerobiosis and the presence of nitrate and nitrite ions. Nitrite -N is denitrified as readily as nitrate -N in alkaline soils but only slowly in acid waterlogged soil (pH 5.8), (Bremner and Shaw, 1958).

2.2.7.2. Ethylene

At low concentrations ethylene gas behaves hormonally on plants. Ethylene (10 p.p.m.) inhibited seminal and stimulated lateral root development in barley (Crossett and Campbell, 1975), and reduced the root growth rate of wheat by 60 per cent at 10 p.p.m. (Smith and Robertson, 1971). This concentration of ethylene virtually inhibited root extension in barley and conspicuous clumps of root hairs developed within 2 mm of the root apices which become swollen (Smith and Russell, 1969).

Ethylene concentrations as high as 24 p.p.m. were detected in sealed soils at field capacity and in waterlogged soils, although field results were variable and sensitive to water movement in the profile. No samples from above watertables were greater than 0.1 p.p.m. (Smith and Russell, 1969). Other saturated and unsaturated simple hydrocarbons and olefins were detected by Smith and Restall (1971) but they concluded that ethylene was the only gas in anaerobic woil which was likely to affect plant growth and they suggested that it is unlikely that strictly anaerobic bacteria are responsible for ethylene production. Smith and Dowdell (1974) detected ethylene at 15 cm depth in an irrigated soil maintained near field capacity with a 6.4% oxygen concentration. Dowdell et al. (1972) detected both ethylene and nitrous oxide having concentrations ranging up to 5 and 2500 p.p.m. respectively at depths of 30 to 90 cms. The addition of glucose and methionine to waterlogged soils stimulates the production of ethylene while other substrates and crop residues may influence ethylene production in soil (Lynch, 1972).

2.2.7.3. Carbon dioxide

The gas immediately above a watertable may be extremely high in carbon dioxide (Enoch and Dasberg, 1971) and falling soil oxygen concentration may be correlated with an increasing CO_2 concentration (Hanan, 1964).

2.2.7.4. Organic Acids

Takijima (1968) detected ten organic acids in flooded paddy soil. Formic, acetic, butyric, lactic and succinic acids were the most abundant and the aliphatic momobasic acids inhibited root elongation.

2.3. THE PHYSIOLOGICAL AND BIOCHEMICAL RESPONSE OF PLANTS TO WATERLOGGING AND REDUCED OXYGEN SUPPLY TO THE ROOTS

2.3.1. Introduction

The physiological and biochemical response of plants to waterlogging and reduced oxygen supply to the roots has been reviewed by van't Woudt and Hagan (1957), Bergman (1959), Stolzy and Letey (1964a, 1964b), Grable (1966), Kramer (1969), Crawford (1972), Stolzy (1972), Rowe (1973), and Russell (1973). A theoretical approach to the oxygen relationships of plant roots has been developed and reviewed by Lemon (1962), Lemon and Wiegand (1962), Luxmoore, Stolzy and Letey (1970 a,b,c,d,) and Luxmoore and Stolzy (1972 a,b)

2.3.2. The oxygen demand of root tissue and the physical and chemical restraints upon supplying that demand

The oxygen demand of root tissue is not uniform along the longitudinal axis of a root. In peas the respiration rate per unit length is greatest between 1 and 2 mm from the root tip which corresponds with the zone of highest dry weight per unit length. The maximum cell volume and maximum respiration per cell are obtained at approx. 5 mm from the root apex (Brown and Broadbent, 1950). In barley the highest oxygen consumption rate per unit volume was in the apical zone and declined to less than half 10 cms from the apex (Machlis, 1944). The oxygen consumption rate in onion roots is 60% higher in the apical 5 mm zone than in sequential 5 mm zones further from the apex. The nitrogen and phosphorous concentration is also higher in the apical zone, but the oxygen consumption per unit of nitrogen or phosphorus showed no trend along the root. (Norris, 1956) Jensen (1955) found the highest protein and total nitrogen concentration in a section 1.5 mm from the root tip in Vicia faba. Berry and Norris (1949a) also found that the apical 0-5 mm segment in onion consumed oxygen at approximately twice the rate of other segments when oxygen was non-limiting, and in limiting conditions the respiration rate was dependent upon the partial pressure and the temperature, but the apex always had the highest rate. Jensen (1960) also reported that a rise of temperature increased the respiration rate of corn and tomato roots. Lemon and Wiegand (1962) and Luxmoore, Stolzy and Letey (1970b) also reported higher respiration rates in the apical 1 cm of a range of species.

Metabolic activity of mustard roots is not inhibited unless the oxygen concentration at the root surface is low (less than 1.0%) (Greenwood, 1968), but Williamson (1968) recorded reductions in root elongation in Vicia faba of 50% at 2.5% oxygen concentration six hours after treatment commenced, and cell division was reduced 80% by oxygen concentrations less than 10% in a 24 hour period. Amoore (1961) reported that mitosis in dividing cells of pea root tips was arrested or retarded at oxygen concentrations less than 0.2%. The diffusion coefficient of roots is highest at the apex (Berry and Norris 1949b).

The requirement of roots for oxygen, particularly at the root tip zone has been described from a theoretical model viewpoint by a number of authors.

Lemon (1962) and Lemon and Wiegand (1962) developed a model to relate the respiration "demand" of roots of varying dimensions to the rate of "supply" of oxygen by diffusion through the surface water film and tissue of root system. They noted that the particular characteristics of a root are related to physiological age and genotype. Luxmoore, Stolzy and Letey (1970 a,b) described a more complex model including allowances for longitudinal diffusion within the root, whereas Grable (1966) and Greenwood (1971) related the oxygen supply to the aeration status of the soil.

All authors concluded that roots of species not adapted to waterlogged soil conditions can be separated from a gaseous oxygen supply by only a small diffusion path length, dependent upon the dimensions of the root, water film thickness and soil structure.

2.3.3. The response of root systems to reduced oxygen supply

2.3.3.1. The measurement of soil aeration

Methods of measuring soil aeration have been reviewed by Grable (1966) and Greenwood (1975). Lemon and Erickson (1952) and Stolzy and Letey (1964a) described the use of a bare platinum electrode to measure oxygen flux, however McIntyre (1970) concluded that the use of electrodes to measure oxygen flux are unreliable, except in saturated porous media with water at zero or positive pressure and the behaviour in 2-phase media cannot be extrapolated to 3-phase media.

2.3.3.2. The response of roots to reduced oxygen concentration

Reducing the oxygen concentration about a growing root affects the elongated rate, developmental pattern mitotic activity and respiration within the root. Geisler (1962) concluded that the major responses of reducing oxygen concentration from 8 to 4 mgm $O_2 l.^{-1}$ about pea roots were reduced root elongation, accelerated initiation of higher order branching and increased number of laterals per unit length. Cotton and soybean roots grew normally with oxygen at 15% to 21% soil air, slower at 10%, and adapt at 3% and 5%. At 2% and less they slow to zero growth. At 0% after 30 minutes death of meristemmatic tissue begins. The first evidence of the effect of low oxygen concentrations is in reduced cell elongation (Huck, 1970). Similarly Eavis (1972) noted that a decline in oxygen concentration from 21% to 8% firstly affected cell elongation and therefore root elongation, but cell division was also reduced at 3%. At partial pressures less than 10%, aerobic respiration was reduced and at 0% anaerobic respiration occurred. Grable and Siemer (1968) described a rapid decline in root elongation in a soil zone where the oxygen concentration fell from 20% to 1%.

Letey and Stolzy and Blank (1962) noted that low oxygen concentrations were most detrimental to corn roots immediately after germination.

Stolzy and Letey (1964a,b) have reviewed results of correlations between root growth and oxygen diffusion rates measured by platinum electrodes in three-phase media. Because of the criticisms of this technique their general conclusion that root growth of a wide range of species is limited in zones of soil with an oxygen diffusion rate less than 20×10^{-8} gm cm^{-2} min^{-1} is questionable but from these studies a number of factors pertinent to root growth under reduced aeration emerge.

There is a lower limit to the oxygen availability to allow successful germination and emergence of seeds. The threshold differs between varieties and species. (Erickson and Van Doren, 1960). Root growth and depth of root penetration of snapdragon was limited in a profile of decreasing oxygen content with depth; the critical oxygen concentration was approximately 2% (Stolzy, Letey et al., 1961). The oxygen requirement of sunflower and cotton roots is higher than for barley and corn. (Letey, Stolzy et al., 1961, 1962; Letey, Stolzy and Valoras, 1965). The critical oxygen flux to permit root growth is independent of root and/or air temperature, but above the critical level root growth rates respond to changes of ambient temperature. (Letey, Stolzy, Valoras and Szuszkiewicz, 1962). Dense subsoils which permit only low oxygen diffusion may limit root penetration. (Bertrand and Kohnke, 1957).

The reduction of oxygen supply to roots may alter the ratio of oxygen to carbon dioxide in the soil. Grable (1966) considered CO_2 concentrations in soil were generally not deleterious to plant roots. Williamson and Splinter (1968) concluded that a low oxygen concentration was more deleterious to tobacco than high CO_2 concentrations when they occur in flooded soil, however Stolwijk and Thimann (1957) reported that the growth rate of roots of _Pisum_, _Vicia_, _Phaseolus_, and _Helianthus_ were inhibited by 6.5% CO_2 in air but _Avena_ and _Hordeum_ were unaffected.

Higher concentrations of oxygen permitted *Pisum* to tolerate high CO_2 concentrations (Glinka and Reinhold, 1962). Goss (1960) concluded that CO_2 can be harmful to the leguminous genera *Glycine*, *Pisum* and *Vicia* in the presence of ammonium nitrogen. *Zea* and *Triticum* were not sensitive. CO_2 concentrations up to 150 mgm l^{-1} in aerated water culture increased the root length and number of laterals of pea (Geisler, 1963).

The roots of soybean tolerate 20% CO_2 even at low oxygen concentrations (7.2%) but root morphogenesis is responsive to changing CO_2 concentration. (Grable and Danielson, 1965 a,b).

2.3.4. The response of whole plants and top growth to reduced oxygen supply

The yield of top growth of plants is affected by the supply of oxygen to roots at rates higher than those which inhibit root growth. The seedling and flowering stages are the most sensitive. (Stolzy and Letey, 1964 a,b).

2.3.5. The effect of oxygen deficiency in the roots upon water absorption and transpiration

A supply of oxygen to the roots is required for both uptake and transfer of water (Grineva and Burkina, 1971). Soil oxygen concentrations less than 8% reduced the transpiration per unit dry weight of snapdragon leaf and wilting occurred (Letey, Lunt et al., 1961). In tobacco, 10% is the critical concentration (Harris and von Bavel, 1957). Imposing anaerobic conditions on tobacco roots reduced water uptake within six minutes and halved the rate in 30 mins. Aeration restored uptake within 6 to 12 mins even after 6 hrs of anoxic conditions (Willey, 1970). Aerating flooded soil prevented wilting and displacing oxygen from soil at field capacity promoted wilting in tobacco. Therefore reducing oxygen supply reduced transpiration and after some hours permanent root damage can occur (Kramer and Jackson, 1954).

2.3.6. The response of nutrient and mineral uptake to oxygen deficiency and waterlogging

Ion uptake and transport to the xylem is under metabolic control and therefore related to the oxygen supply to metabolizing root tissue (Browner, 1965).

The effect of reduced oxygen tension upon the nutrient and mineral uptake under conditions of low oxygen concentration or waterlogging has a similar pattern for a wide range of species regarded as sensitive to waterlogging. In Table 1 a number of references are summarized.

Rowe (1973) in his review comments that the quantitative significance of this aspect of waterlogging is largely unknown, despite the numerous reports of nutritional changes resulting from waterlogging.

2.3.7. Biochemical changes and production of autotoxic substances in plants as a result of waterlogging

2.3.7.1. Introduction

The effect of waterlogging upon plants, which depend upon diffusion of oxygen to respiring root tissue, is to inhibit aerobic respiration and modify metabolic processes. McManmon and Crawford (1971), Crawford (1972) and Rowe (1973) have reviewed these responses.

2.3.7.2. Glycolysis induced by anoxic conditions in the roots

Reduced oxygen supply to roots induces glycolytic respiration and the production of ethanol. Kenefick (1962) detected ethanol in the roots of sugarbeet under anaerobic conditions. The concentration of ethanol in the xylem exudate of tomato increased as the oxygen diffusion rate in the soil decreased, particularly below 15 x 10^{-8} gm cm^{-2} min^{-1}. Accumulation of ethanol continued while anoxic conditions were applied and was highest in flowering plants and plants growing in bright light. The ethanol concentration could become toxic (Fulton and Erickson, 1964). High ambient air temperatures, high light intensities and cyclical soil temperatures increased the rate of ethanol production in flooded tomato plants and after 12 hours the highest ethanol concentrations were in the base of the stems and top of the root system. (Bolton and Erickson, 1970). Crawford (1966) reported the accumulation of ethanol in roots of races of races of *Senecio* adapted to dry sites when grown under waterlogged conditions.

TABLE 1.

The effect of reduced oxygen supply upon the uptake of nutrients and minerals by species considered sensitive to waterlogging.

SPECIES	ELEMENTS HAVING REDUCED UPTAKE RATES	NO CHANGE IN UPTAKE	ELEMENTS ACCUMULATED	REFERENCE
Hordeum vulgare	K,P	Ca,Mg	Na	Letey, Stolzy et al., (1962)
Gossypium) *Helianthus*)	K,N,P,Ca,Cl	-	Na	Letey, Stolzy et al., (1961)
Zea mays	K,N,P	Cl	Na, Ca, Mg	Letey, Stolzy and Valoras (165)
Zea mays	K, Ca, Mg, N, P	-	-	Lawton, (1946)
Tabaccum sp.	K,N,P,Mg,Ca	-	-	Harris and Van Bavel, (1975)
Tomato, tobacco, soybean	K, Ca, P	Mg, Fe, Mn	Na	Hopkins, Specht and Hendricks, (1950)
Citrus	N,P,K,Ca,Mg,Cl, Zn,Cu,Mn,B,Fe	-	Na	Labanauskas et al., (1966)

2.3.7.3. The effect of waterlogging upon enzyme activity in roots

Waterlogging inhibits the citric acid cycle and reduces the rate of respiration and metabolism of carbohydrate in tomato (Fulton, Erickson and Tolbert, 1964). In corn seedlings an anaerobic environment increased the activity of alcohol dehydrogenase and depressed the activity of cytochrome oxidase. Pyruvic acid and acetaldehyde were metabolized and ethanol was not, suggesting anaerobic conditions inhibit the Krebs citric acid cycle, causing the accumulation of pyruvic acid, which is decarboxylated to acetaldehyde, and subsequently dehydrogenated to ethanol (Hageman and Flesher, 1960). Crawford (1966) reported increased anaerobic respiration in races of *Senecio* from dry sites when waterlogged. The activity of malic dehydrogenase was increased in non-helophytic *Senecio* species (Crawford and McManmon, 1968).

Alcohol dehydrogenase activity increased in flooded roots of *Trifolium subterraneum* and reached maximum values within one week from flooding (Francis, Devitt and Steele, 1974).

Succinic acid accumulated in non-helophytic species (Crawford and Tyler, 1969). In peas, anaerobic conditions caused an increase in the concentration of lactic and succinic acid and ethanol and a reduction in malic and citric acid. Acetic and pyruvic acids were unaffected (Wager, 1961).

2.3.8. The effect of waterlogging upon plant hormone synthesis

The relationship between waterlogging of root systems and plant hormone synthesis, translocation and activity is discussed in the reviews of Rowe (1973) and Grable (1966).

In sunflower, the translocation of auxin from shoot to root is affected by waterlogging. Phillips (1964a) presented evidence for the translocation of auxin from the shoot into the root of sunflower growing in an aerated root environment, but flooding increased the auxin level within the shoot.

The concentration of an auxin, behaving chromatographically similar to indole-3-acetic acid, in the shoots of waterlogged plants increased three fold in 14 days (Phillips 1964b).

The cytokinin content of ascending sap in flooded sunflower was reduced, together with the rate of exudation from the roots, amino acid transport from the roots and metabolic activity in the root apex (Burrows and Carr, 1969). They suggest the decrease in kinetin supply may be partly responsible for accelerated senescence of lower leaves after 72 hours of flooding. Seth and Wareing (1965) isolated a kinin-like factor from Phaseolus vulgaris. Cytokinins stimulate transpiration by maintaining stomatal opening and therefore reduced transpiration may be associated partly with kinetin metabolism (Luke and Freeman, 1968). Rowe (1973) reviewed the possible physiological effects of reduced kinetin activity.

Reid, Crozier and Harvey (1969) showed that waterlogging the roots of tomato inhibited stem growth and reduced the export of gibberellic acids from the root to the shoot in the xylem sap. After one day the reduction was 40 fold and after three days there was no detectable activity. They suggested that the decline in growth rate of shoots after flooding may, in part, be due to reduced supply of gibberellins to the shoot and in a further study (Reid and Crozier, 1971) application of GA_3 to shoots alleviated the symptoms of flooding for four days, after which they suggest other factors become important.

The concentration of the biologically active hydrocarbon, ethylene, increased in the submerged portions of sunflower and tomato within 24 hours (Kawase, 1972). Waterlogging broad bean plants (Vicia faba) caused a rapid four fold increase in endogenous concentration of ethylene in the stems and leaves. (El-Beltagy and Hall, 1974). They suggest that the source of ethylene may be protein breakdown with methionine as a possible precursor, rather than a result of auxin action which accumulates at a slower rate after flooding.

The presence of ethylene and asymetric distribution of auxin in roots may cause tropisms of root orientation and growth (Pratt and Goeschl, 1969).

2.3.9. The effect of waterlogging upon nitrogen fixation in leguminous species

In a review of the biochemistry of symbiotic nitrogen fixation in legumes. Bergersen (1971) emphasised the need for oxygen supply to nodules. At low oxygen partial pressures nitrogen fixation in detatched soybean nodules became less efficient and the respiration quotient (CO_2:NH_3 ratio) increased, signifying a decrease in N-fixation rate. He suggests the main role of oxygen is most likely to be in the supply of ATP to the nitrogen fixing system through oxidative phosphorylation and even at atmospheric partial pressures the concentration of oxygen is limiting for detatched nodules.

The immersion of detatched soybean nodules in water inhibited acetylene reduction by reducing the oxygen supply to the nodules. In a shaken oxygenated aqueous medium acetylene reduction occurs. (Sprent, 1969).

The products of nitrogen fixation in legume nodules undergo transamination reactions within the nodules, are concentrated in the endodermic and pericyclic cells of the nodule vascular tissue and are then translocated to the growing parts of the plant mainly as glutamine, asparagine and aspartic acid. (Pate, 1962; Page, Gunning, and Briarty, 1969).

Waterlogging and reduced oxygen concentration affects the formation, development, size and activity of nodules in leguminous species. In garden pea (Pisum sativum, L. cv. Meteor), waterlogging decreased nodule tissue production and the specific activity of nitrogenase to approximately one third of the activity in aerated controls. The effect was most marked three or more centimetres below the water surface. Plants reliant on symbiotic nitrogen supply were more affected by flooding than NO_3 -N supplied plants, suggesting a high sensitivity of symbiotic fixation to excess water in the root environment. Nodules below 3 cms into the waterlogged zone showed marked necrosis and degeneration of bacterial tissue and the reduced formation of vascular transfer cells believed to be active in the excretion of products from the nodule (Minchin and Pate 1975). Virtanen and von Hausen (1963) recorded small nodules and poor plant growth on pea plants in non-aerated culture solution, although nodulation was abundant. Also Bond (1950) grew soybean in a series of low oxygen environments in culture solution and noted that the number of nodules initiated was not reduced, but the weight of nodules, plant weight and nitrogen concentration in the plant were reduced, indicating fixation is more sensitive than nodule initiation to low oxygen concentrations. However, in regions of soil having low oxygen diffusion rates nodulation of _Trifolium subterraneum_ var. 'Bacchus Marsh' was inhibited, with nodule formation restricted to the better aerated surface layers of soil (Loveday, 1963). In partially waterlogged and oxygen deficient soil, the acetylene reduction activity of nodules on _Vicia faba_ was lower than the maximum activity which occurred at field capacity (Sprent, 1972). Nodules above a free water surface were necessary for improved plant growth of peas (Virtanen and von Hausen, 1935). Under poorly aerated soil conditions five native leguminous species had reduced nodulation (Diatloff, 1967). All the above species are regarded as sensitive to waterlogging.

The nodules of red clover, a species moderately tolerant of flooding, are formed at highest density at 5% oxygen concentration and can develop normally to the same weight over a 5% to 21% oxygen concentration range, but any reduction of oxygen supply below that available at 21% caused a significant reduction in yield of nodulated plants (Ferguson and Bond, 1954).

2.4. THE ADAPTIVE MECHANISMS OF PLANTS TOLERANT TO WATERLOGGED SOIL CONDITIONS

2.4.1. Oxygen diffusion within the plant to the roots and from the roots into oxygen deficient media

The root tissue of plants has within it air spaces which differ between species, variety, the type of root and the environment in which the roots develop. The proportion of air space or porosity of plant tissue particularly of root tissue is related to the relative tolerance of species and varieties to waterlogging (Stolzy, 1972).

Jensen, Luxmoore, van Gundy and Stolzy (1969) showed that the porosity of the stems of species not tolerant to flooding (Phaseolus vulgaris and Pisum sativum) and a tolerant species (Oryza sativa) were all high (18.5% to 38.3%) but only the roots of the latter species, rice, had a high root porosity (26.5%), whereas root porosities of the intolerant species were approximately 4%.

The root porosity of both tolerant and intolerant species were higher when plants were grown under flooded conditions than under non-flooded conditions, but porosities were similar in aerated and non-aerated solution culture, indicating that root contact with free water was a critical factor in inducing higher porosity. (Varade, Letey and Stolzy, 1970, 1971; Luxmoore and Stolzy 1969).

This conclusion contrasts with Bryant's (1934) observation that the cortex of barley grown in aerated culture solution contained uniformly packed parenchyma cells whereas under non-aerated conditions large air spaces separated by narrow bands of parenchyma developed in the xylem. Also thickening closer to the root tip and thinner root walls occurred. Pradham, Varade and Kar (1973) showed that the root porosity of rice increased markedly as the soil approached saturation and became flooded and submerged to a depth of 6 cms.

Rice roots in flooded soil were larger, less branched and had fewer root hairs (Valoras and Letey, 1966). Tomar and Ghildyal (1975) described the morphological differences between the solidly packed cellular structure of rice under non-flooded condition and large porous areas suggesting degradation of root cortex cells in flooded plants.

Root porosity in wheat is also influenced by light intensity, oxygen in the culture solution and variety (Varade, Stolzy and Letey, 1970) and in rice by light intensity (Varade, Letey and Stolzy, 1971).

The porous structure of roots permits the presence within the root of gases, particularly oxygen, which can be used in respiration and metabolic functions. Van Raalte (1940) analysed the gases in air spaces in rice roots and concluded that they depended upon the movement of oxygen from the leaves along a concentration gradient from the basal portion of the roots to the root tips. Greenwood (1967) studied the oxygen concentration at the root surface of vegetable species grown as seedlings in an anoxic medium and concluded that the rapid transport of oxygen from tops to roots was consistent with a structure of non-tortuous gas filled channels in the tops and roots through which oxygen moved downwards by diffusion. Greenwood and Goodman (1971) concluded that the oxygen requirements of short roots growing into anoxic media could be met by diffusion, but if the partial pressure at the root surface was raised to .05 atmospheres the requirements could be met from the surrounding medium.

The diffusion of oxygen through the roots of plants not adapted to waterlogged conditions partially compensates for anoxic conditions in the root medium. In pea seedlings radicles maintained at zero oxygen concentration could maintain a growth rate of approximately one fifth of the rate in an aerated medium, but the growth rate was retarded at all root medium oxygen concentrations less than atmospheric equilibrium suggesting that in this species intraplant diffusion is inadequate and of minor importance compared with oxygen supply through the soil pathway. (Eavis, Taylor and Huck, 1971)

Evans and Ebert (1960) studied the diffusion of oxygen down the root of Vicia faba and concluded that the movement was consistent with that through a continuous narrow gas space with side walls highly impermeable to sideways diffusion because no structure was found large enough to allow for both longitudinal and sideways diffusion. Ebert and Howard (1961) concluded that in some species the gas spaces reach the meristem but do not penetrate it sufficiently to oxygenate all meristematic tissue, thus inhibiting root growth. The porosity and oxygen diffusion coefficient in rice roots are much higher than in barley and corn roots and the root wall permeability is much lower (Jensen, Stolzy and Letey, 1967). They calculated the partial pressure which would be present at the tips of roots of varying length and conclude that the structure of rice roots would permit adequate oxygen to be supplied to the meristems of long rice roots, whereas in corn and barley the partial pressure would fall quickly and diffusion would only satisfy the requirements of roots only a few centimetres long, thus rendering the root tips of longer roots in these species dependent upon external oxygen. Barber, Ebert and Evans (1962) also concluded that the porosity in rice (5-30%) and barley (less than 1%) permitted oxygen diffusion consistent with continuous gas spaces, but the rates were dependent upon porosity.

Luxmoore, Stolzy and Letey (1970b) reported that the wall permeability of rice is lower than for maize and the porosity rises linearly in the apical 6 cms of rice to a stable value of 30% whereas it rises to only 9% in the same root segment in maize and from related studies Luxmoore et al., (1970d, 1972a, 1972b) concluded that modification of porosity is a key factor in the design of root systems with high adaptability to a wide range of soil aeration conditions because roots with a higher porosity had a higher oxygen concentration within the root and at the root tip and were less dependent upon soil aeration.

In studying the relative tolerance of Strawberry and Ladino clovers to waterlogging and flooding, Bendixen and Peterson (1962) found that stolons of strawberry clover grown under natural conditions are able to transport sufficient oxygen either basipetally or acropetally to allow growth six inches from the oxygen source. Courser roots developed on Strawberry clover under flooding. Air spaces which allow the marsh grass, *Spartina alterniflora*, to survive in anoxic mud were reported by Teal and Kanwisher (1966) and Coult (1964) suggested that the aerenchyma in the rhizomes of the bog species *Menyanthes trifoliata* are a morphological adaptation to allow sufficient volume of oxygen for the maintenance of the surrounding tissue.

Armstrong (1964) reported that *Menyanthes trifoliata* and two other British bog species, *Eriophorum angustifolium* and *Molinea coerulea* oxygenate the medium surrounding the roots by diffusion of oxygen from the tops into the roots and then into the medium. The root tip was associated with the highest diffusion rate, and the rates from the species were correlated with their adaptation to waterlogging. In a further study of oxygen diffusion from the roots of ten species of bog plants, the diffusion rate measured suggested there is a negligible barrier to diffusion between the intercellular spaces and exterior of the root, and that the rate is governed by the oxygen concentration in the root. As the diffusion rate is highest in the apical zone of the roots it is possibly an adaptive mechanism to provide external oxygen to the meristem of the root. Suberization of the epidermal layers in the non-apical zone may cause lower permeability to oxygen release. The high rate of oxidation outside the roots of some species suggests that enzymatic oxidation may be occurring in the oxygenated zone around roots (Armstrong, 1967b). The size of the oxygenated layer corresponds to the tolerance of species to reducing conditions caused by waterlogging (Armstrong 1970) and it prevents reduced toxins from reaching the root (Armstrong 1967,b; Engler and Patrick, 1975; Jones, 1975) and corresponds with differences in susceptibility of rice to a physiological disease (Armstrong, 1969).

Oxygen also diffuses from the roots of woody species. In species of *Salix* and *Myrica gale* oxygen enters the roots through the bark immediately above the watertable (Armstrong, 1968). Oxygen diffuses from the roots of the non-helophytes *Zea mays* into the surrounding medium (Jensen, Letey and Stolzy, 1964).

The occurrence of high levels of carbon dioxide in soil can reduce the downward diffusion rate of oxygen and thereby adversely affect growth (Webster, 1962).

2.4.2. The formation of adventitious root systems and changes in root distribution

The formation of adventitious roots, originating from near the stem base of a plant which is waterlogged, and their growth predominantly in the surface layer of the waterlogged medium is a morphological phenonemon commonly associated with plants tolerant to waterlogging.

Weaver and Himmel (1930) studied the response of four species to poor aeration in saturated soil conditions. A shallow, fine and much branched root system which had a high surface to volume ratio developed under waterlogged conditions. The root depth decreased with increasing soil water content and root hairs were absent in free water. Cannon (1940) described two forms of adventitious roots. Firstly a slender much-branched form growing near the surface which lacked prominent intercellular spaces and which probably derived their oxygen supply from the thin oxygenated surface layer in which they grew and, secondly, thick roots bearing few laterals which penetrate deeply into the soil. In *Carex limosa* these roots contain 10 to 15 rows of radially arranged intercellular air spaces allowing oxygen diffusion. Caughey (1945) reported a surface "mat" of roots developing from bog shrub during periods of high water-table and Kramer (1951) observed adventitious roots forming on sunflower above the soil surface in the second or third day after flooding. The development was more pronounced in plants flooded in water than flooded in soil. He suggested that plants which survive flooding long enough to establish a surface adventitious root system persist longer although checked severely. Jackson (1955) found that sunflower and tomato plants which developed adventitious roots recovered quicker from flooding than those which did not develop such roots, or from which such roots were removed.

Rice plants which are established under non-flooded conditions became chlorotic and tended to wilt when flooded until new advantitious roots developed at the base of the plant and grew into the flooded medium. (Varade, Letey and Stolzy, 1970; Valoras and Letey, 1966). These roots are thicker, less branched and have fewer hairs (Valoras and Letey, 1966) and eventually contribute most to root weight (Luxmoore and Stolzy, 1969). Later in the life of rice plants after stem elongation, diffusion from the leaves is restricted and the oxygen supply to the deeper roots is from a mat of fine roots formed at the water surface after tillering (Alberda, 1953).

The initiation of adventitious roots in flooded sunflower plants approximately 14 days after flooding is possibly the consequence of the basipetal translocation of initiating factors (including auxin) from the upper parts of the shoots concentrating to active levels at the base of the stem within a few days of flooding (Phillips, 1964a,b). Varga and Humphries (1974) attributed enhanced root formation on petioles of dwarf bean to local high concentrations of indole-acetic acid stimulated by gibberellic acid in the leaf laminae. Adventitious root formation was enhanced by tryptophan, which is considered to be a precursor of IAA and is inhibited by cytokinins which slow the release of tryptophan from protein.

Ethylene, acetylene and propylene at high concentrations stimulated adventitious roots in a number of species (Zimmerman and Hitchcock, 1933) and auxin induced production of ethylene in pea roots caused an increase in the weight to length ratio of the roots (Chadwick and Burg, 1967).

2.4.3. Biochemical adaptation of plants to waterlogged conditions in the root zone

2.4.3.1. Non-accumulation of toxic ethanol concentrations

Crawford (1969) proposed that morphological explanations of flooding tolerance are inadequate and proposed a scheme whereby species intolerant of flooding undergo accelerated glycolysis and the production of toxic ethanol concentrations whereas tolerant species avoid this accumulation and switch metabolically from ethanol to malate production. Crawford and Tyler (1969) reported that malate accumulated in helophytes and was depleted in non-helophytes under waterlogging. Ethanol did not accumulate in tolerant races of *Senecio* (Crawford 1966). The activity of alcohol dehydrogenase was not increased and ethanol accumulation was homeostatic in seven helophytes studied by Crawford (1967). Three helophytes accumulated malic acid in quantities comparable to ethanol in non-helophytes. The ethanol production was caused by induction of alcohol dehydrogenase in non-helophytes.

McManmon and Crawford (1971) and Crawford (1972) have proposed that the absence of functional malic enzyme from helophytes prevents the conversion of malic acid to pyruvic acid and thereafter to acetaldehyde and ethanol.

2.4.3.2. The adaptive significance of the activity of alcohol dehydrogenase

Alcohol dehydrogenase is the enzyme involved in converstion of acetaldehyde to ethanol as the last step in the glycolytic sequence. McManmon and Crawford (1971) found a strong correlation between ADH activity and flooding tolerance in 19 species.

In the legumes Pisum sativum and Vicia faba activities increased 15.6 and 5.0 times respectively whereas in Phalaris arundinacea activity decreased 70 per cent. A fall in the value of the Michaelis constant for ADH upon flooding in tolerant species indicated either a change in the alcohol dehydrogenase enzyme or activity dependent upon acetaldehyde concentration.

Marshall, Broué and Pryor (1973) correlated the sensitivity of maize to flooding with allelic forms of alcohol dehydrogenase (Adh). Plants of the Adh^f (fast form having a higher specific activity than an Adh^s slow form) were more sensitive to flooding for 10 days. Intermediate activity between the adh^f adh^f and Adh^s Adh^s levels suggests the formation of a heterodimeric ADH molecule in the heterozygote Adh^f Adh^s. In germinating seeds of narrow leafed lupin three alcohol dehydrogenase isozymes are present resulting from two homodimers of two independent loci, Adh_1 and Adh_2 and a heterodimer. In flooded roots only the Adh_1 isozymes are present indicating flooding induces Adh_1 but suppresses Adh_2. Schwartz (1969) proposed that short periods of anoxia during germination actively select and maintain Adh elleles for highly active alcohol dehydrogenase in maize populations by allowing the release of energy through anaerobic respiration. In rice alcohol dehydrogenase activity is induced by anaerobic conditions, is proportional to ethanol concentration and unresponsive to or is decreased by acetaldehyde. Therefore alcohol dehydrogenase in this species actively catabolizes ethanol under anaerobic conditions (App and Meiss, 1958). Ethanol can be catabolized in some plant tissues (Cossins and Bewers, 1963; Castelfranco, Bianchetti and Marne, 1963).

The activity of alcohol dehydrogenase varies between the leguminous genera Pisum, Vicia and Lens although the molecular weights are similar (Leblova and Mancal, 1975), and genotypes and subspecies of Trifolium subterraneum express different activities of alcohol dehydrogenase under flooding. The flooding tolerant genotypes of the subspecies yanninicum have lower activities (Francis, Devitt, and Steele, 1974).

2.4.3.3. The adaptive significance of nitrate reductase and amino acid synthesis

Flooding markedly increased the nitrate reductase activity in roots and leaves of flooding - tolerant species whereas in intolerant species the activity generally declined. In six tree species the ability to increase the production of amino acids (aspartic acid, glutamic acid, alanine and citruline) is matched exactly by the flooding tolerance of the species. (Garcia-Novo and Crawford, 1973). They propose that nitrate reduction provides an alternative to oxygen as an electron acceptor, facilitating the survival of flood-tolerant species during periods of anoxia. The amination of pyruvate and other products of glycolysis and translocation of amino acids to the shoot transfers the "oxygen debt" of the roots to the aerated shoots. Nitrate reductase activity is present in uninoculated pea roots (Wallace and Pale, 1965) and in a high proportion of a large number of woody species the ascending nitrogen is entirely in organic form, mainly as aspartic acid, glutamine and asparagine (Bollard, 1967).

2.4.3.4. Absence of precursors of toxic substances

In the fruits peach and plum a cyanogenic glycoside is present which under waterlogging of the roots releases hydrogen cyanide which inhibits metabolic oxidation and catabolism of ethanol. In pear, which is tolerant to waterlogging, the glycoside is absent (Rowe, 1968).

2.4.4. Mineral accumulation in species tolerant to waterlogging

In contrast to the changes in mineral and nutrient absorption by waterlogging in flooding sensitive species, flooding of non-sensitive species either does not affect accumulation of nutrients e.g. Na,Cl, N,P,K. Ca and Mg in rice (Valoras and Letey, 1966), Mn in lowland rice (Clark, Nearpass and Specht, 1957) or else the species tolerate high ionic concentrations.

Some Carex species tolerate 8 - 14,000 p.p.m. Mn^{++} and Fe^{++} ions were either tolerated or not accumulated (Jones, 1972 a,b).

2.5. THE ADAPTABILITY OF SPECIES USED IN AGRICULTURAL SYSTEMS TO WATERLOGGING, HIGH WATERTABLES AND FLOODING

2.5.1. The adaptation of lucerne to waterlogging, flooding and high watertables

2.5.1.1. The effect of the duration of flooding on lucerne growth

Lucerne, Medicago sativa and its relations, is regarded as a species which is more sensitive than most pasture species to poorly aerated soil conditions caused by waterlogging, flooding or high watertables.

In a study of the flooding tolerance of nine leguminous pasture species, including Medicago media cultv. 'Rambler' in pots as eight week old seedlings, yellowing of leaves and root decay were evident in the lucerne after ten days and the yield of herbage dry matter was reduced approximately 50% at the first harvest (5 days). The dry matter yield of roots was reduced 60% within 5 days and 90% after 20 days. It was considered this lucerne cultivar could tolerate waterlogging for 15 days (Heinrichs, 1970). Rogers (1974) measured the response of five lucerne cultivars to waterlogging and two levels of evaporation deficit and reported intervarietal differences to waterlogging for 10 days. Yield depressions were 'Hunter River', 69.2%; 'Du Puits', 70.8%; 'Peruvian P10', 68.2%; 'Siro Peruvian', 48.8% and Lahontan 39.7%. Waterlogging reduced the nitrogen content of the herbage but did not reduce the phosphorus content or increase the manganese content. Plant density was reduced in all varieties by waterlogging after only ten days and frequent irrigation caused rotting of the taproot.

Finn, Bourget, Nielsen and Dow (1961) included lucerne in a study of the effect of varying moisture suctions (0,25,40 cms) applied for 10, 20 and 30 days on the regrowth of herbage and roots. Lucerne grown at zero moisture tension (waterlogged) for 10 days did not recover after sixty days of regrowth.

The regrowth of roots after all flooding periods was low, but top growth recovery was better after shorter periods than long periods of flooding.

2.5.1.2. The sensitivity of lucerne roots to waterlogging

Lucerne is particularly sensitive to increased temperature in the root zone during flooding. Increasing the temperature of flooding water from 5°C to 26°C reduced the growth and yield of lucerne flooded for only one week (Finn, Bourget, Nielsen and Dow, 1961). The lucerne cultivar 'Rambler' when grown under varying root zone temperatures at constant air temperature does not grow for more than 14 days, and herbage regrowth, the weight of crowns and root dry matter are reduced after 7 days flooding irrespective of the root temperature regime. However at lower root temperatures, the percentage survival of plants is higher and the decay of roots is less after flooding up to 28 days (Heinrichs, 1972). The plant density of 'Hunter River' lucerne, grown at 33°C and flooded immediately after cutting was reduced by 85%; flooding 5 days after cutting killed 35% of plants, but at 21°C no plants were killed and delayed flooding alleviated the severe check to growth caused by flooding immediately after cutting (Cameron, 1973). In the same paper he reported intervarietal differences in flooding tolerance. 'Hunter River' lucerne was more seriously affected by flooding than the cultivars 'Rhizoma' and 'Lahontan'. High root zone temperatures during flooding severely affected all cultivars, but high air temperatures did not affect the reaction to flooding.

High soil temperatures and reduced aeration cause necrotic condition and root rot to develop quickly. Roots flooded at 25°C for 18 hrs. are undamaged, but as the temperature is increased the necrotic and rotting symptoms develop very quickly (Erwin, Kennedy and Lehman, 1959).

Lucerne varieties are sensitive to excessive soil moisture and reduced aeration caused by excessive irrigation or high fluctuating watertables. Wahab and Chamblee (1972) reported a decline in lucerne plant population caused by the excessive soil moisture conditions resulting from precipitation after irrigation. Intervarietal differences were striking.

The varieties 'Du Puits' and 'Cherokee' were almost completely killed in one year whereas the variety 'Bonanza' was less affected.

Under static watertable condition maximum yields of lucerne were obtained at a watertable depth of 60 cms (Tovey, 1964). Under these conditions he reported that some roots extended into the saturated zone above the watertable and that some enlarged white rootlets extended into the watertable, and he observed that in the glasshouse alfalfa root systems will adapt to shallow constant level watertables. Fox and Lipps (1955) described the distribution of lucerne roots associated with watertables in various profiles and in one soil an abundance of white fibrous roots was obtained from immediately above and in direct contact with the watertable and in another soil numerous white turgid fibrous roots were found more than 30 cms below the free water surface. Therefore if lucerne plants of the varieties in these studies have portion of their root system aerated above a static watertable some root adaptation to poorly aerated and waterlogged conditions can occur. However fluctuating watertables affect yield. Tovey (1964) studied the effect of raising a 60 cm watertable to the surface for up to 11 days on lucerne yield. Three days of flooding increased yields in the following three cuts above the control, but four or more days flooding reduced yields and subsequent regrowth. Flooding for over one week virtually destroyed the lucerne stand by causing serious deterioration of roots and crowns especially during hot weather. Watertable depths less than 40 cms reduced lucerne yield in the study of Jensen and Lesperance (1971). At 10 and 20 cms depth the yields were approximately 11% and 45% of those for watertable depths greater than 40cms. Rai, Miller and Hittle (1971) found the highest yields of two lucerne varieties 'Narragansett' and 'Kentucky Syn 2' at a watertable depth of 45 cms and that raising the level of water to 15 and 30 cms reduced yields and caused root rotting below those depths. Soil water suctions consistently less than about 20 centibars reduced the yield of lucerne under irrigation in the Imperial Valley, California (Lehman, Richards, Irwin and Marsh, 1968).

2.5.1.3. The effect of submersion on lucerne

Bolton and McKenzie (1946) considered that 'Grimm' lucerne could only be submerged by spring flooding for 10 to 14 days without causing excessive permanent injury.

The sensitivity to flooding is higher under high average daily temperature conditions. 21 days of submersion were tolerated by 'Ladak' lucerne at 4°C but at 8° C 40% of plants were permanently injured (McKenzie, 1951).

2.5.1.4. The effect of waterlogging on iron, manganese and aluminium uptake by lucerne

The concentration of manganese in the leaves, petioles and growing points of waterlogged lucerne occurs within a few days. The symptoms of manganese toxicity are lighter colour of growing points and chlorosis on tips of younger leaves associated with manganese accumulation in the growing points. The roots, crown and stem do not accumulate manganese to the same level as the leaves and apices (Graven, Attoe and Smith, 1965). They suggest that the long term effect of manganese toxicity may be more serious than short term anoxic conditions resulting from flooding for only a few days.

The rate of translocation of manganese and aluminium from roots to tops differs between lucerne clones, although the total absorption is similar. The more tolerant clones, which have lower translocation rates, contain more total and water-soluble calcium and the ability to keep calcium in an active form may be an important factor determining tolerance to manganese and presumably aluminium (Ouellette and Dessureaux, 1958b). A toxic concentration (25 p.p.m.) of manganese in sand culture does not equally depress the yield of all lucerne varieties and crosses to the same extent (Dessureaux and Ouellette, 1958a) and a response to selection for tolerance to manganese resulting in more yield and less growth retardation was found by Dessureaux (1958).

Graven Attoe and Smith (1965) found that waterlogging did not greatly affect the iron (Fe^{++}) content of lucerne except for a slight rise in the concentration in the roots. Bartlett (1961) reported that the roots of the lucerne cultivars 'Du Puits' and 'Narragansett' did not affect the Fe^{++}ionic concentration in a nonaerated solution culture whereas species more tolerant of poor drainage oxidized ferrous ions in their root rhizosphere zone.

2.5.2. The adaptation to high watertables and waterlogging of species, other than lucerne, which are used in agriculture

2.5.2.1. The effects of a high watertable on crop and pasture species

The responses to high watertables for cereals, grasslands, pastures, tuberous crops fruit trees and vegetables were reviewed and summarized by van't Woudt and Hagan (1957). They concluded that the damage caused by flooding of agriculturally utilized species is dependent upon the species, duration of flooding, the ambient temperature, the stage in plant growth and relation to dormant periods. An optimum level of watertable seems to exist for each particular crop under given conditions. Williamson and Kriz (1970) reviewed the response of agricultural crops to fixed watertables, fluctuating watertables, deep watertables and temporary surface flooding and waterlogging at or above the soil surface and also concluded that the response is dependent upon species, locality, soil characteristics and the dynamics of the water regime during the growth of the species. Both reviews concluded that most species used in agriculture require a zone of aerated soil for optimum production. The depth of this zone is related to the species and only some species adapted to waterlogged environments can tolerate non-aerated soil conditions in the long term.

Deep rooted species, e.g. corn, require deep watertables whereas shallow rooted species, e.g. soybean and grain sorghum, require shallow watertables for optimum production (Williamson, 1964; Williamson and van Schilfgaarde, 1965). Nicholson and Firth (1953) found that there was an interaction between optimum watertable level and yield which depended upon seasonal rainfall patterns but for a range of eight crop species the optimum level was between 50 and 90 cms. This adaptation is strongly related to soil aeration (Grable, 1966) and Williamson, Willey and Gray (1969) showed that watertables less than 30 cms below the surface in a sandy loam reduced oxygen concentrations in the soil almost linearly from 21% at the surface to 0% at the watertable.

Baumann and Klauss (1955) studied the root distribution of forty two grass species in soil with a watertable at 36 cms deep. Most species had over half of their root system in the top 12 cms of soil and twenty six species had from 4.3 to 0.4% of their root system below the watertable. Prominent agricultural species in this category were Lolium multiflorum (Westerwolds), Festuca arundinacea and Phalaris arundinacea. Ten species grew down to the watertable and six were shallow rooted. In a study of the effect of ground water level upon the productivity of fenland grass Eden et al. (1951) reported lower yields, protein yields and protein contents and depressed K, Mg and Cl content at high watertables.

Ladino clover, orchard grass and tall fescue are adapted to a shallow watertable (15cms) but in combination with surface watering only Ladino clover increased in yield although the grasses had more roots below the watertable level (Gilbert and Chamblee, 1959). Williamson and Willey (1964) found most roots of tall fescue in the top 10 cms of soil over watertables at various depths.

Grain legumes generally require aerated, freely drained soil conditions. The roots of peas extend almost to a watertable and then stop growing; under low oxygen supply they are thicker with reduced laterals and less nodules, and poor aeration reduces N,P and K accumulation but Ca and Mg content increase (Cline and Erickson, 1959).

Optimum watertable depths differ for soybean varieties and the shallow rooted kidney bean gave a maximum yield over a 15cm watertable. The optimum watertable depths differ for soybean varieties and the shallow rooted kidney bean gave a maximum yield over a 15 cm watertable. The optimum depths are also temperature dependent (van Schilfgaarde and Williamson, 1965). Snapbean yields were optimum over deeper watertables in fine soils (Goins, Lunin and Worley, 1966), and the mean air content of the soil was the parameter most highly correlated with yield from *Phaseolus vulgaris* (Dasberg and Dakkar, 1970)

Natural vegetation also differs in soil aeration requirement. Poel (1960b) correlated the soil aeration status with the distribution of species in or away from marshy areas and correlated the distribution of bracken fern with well aerated sites (Poel, 1961).

2.5.2.2. The effect of waterlogging on pasture species other than lucerne

2.5.2.2.1. Leguminous species

A number of leguminous pasture species are regarded as tolerant of waterlogged soil conditions. Marshall and Millington (1967) found that cultivars of *Trifolium subterraneum* subsp. *yanninicum*, *Trifolium repens* and *Trifolium fragiferum* tolerated 21 days of waterlogging without serious reduction in herbage or root yields whereas varieties of *T. subterraneum* subspps. *brachycalycinum* and *subterraneum* and *Ornithopus sativus* were susceptible. Francis and Devitt (1969) also concluded that the order of waterlogging tolerance of subterranean clover subspecies was: *yanninicum* greater than *subterraneum* greater than *brachycalycinum*. Many surface roots were observed on varieties of subsp. *yanninicum* but not the other subspecies and that the isoflavone concentration was inversely related to tolerance to waterlogging. The reduction in accumulation of nutrients is least in the tolerant subspecies *yanninicum* and is correlated with general subspecific performance under waterlogging (Devitt and Francis, 1972).

Heinrichs (1970) considered that birdsfoot trefoil (*Lotus corniculatus*), white clover (*Trifolium repens*) and strawberry clover (*T. fragiferum*) could tolerate flooding for 20 days; red clover (*T. pratense*), as like clover (*T. hybridum*) and lucerne for 15 days and sweetclover (*melilotus alba*), cicer milk vetch (*Astragalus cicer*) and sainfoin (*Onobrychis viciaefolia*) for 10 days or less. In a further study Heinrichs (1972) demonstrated that the relative tolerance of trefoil, lucerne and sainfoin is correlated with the resistance of crowns and roots to degeneration and rotting caused by flooding. Jensen and Lesperance (1971) found trefoil tolerant of poorly aerated soils and Finn et al. (1961) suggest ladino white clover is more tolerant than birdsfoot trefoil and Wahab and Chamblee (1972) reported that ladino clover was not affected by excessive irrigation for two years but a crown vetch (*Coronilla varia*) population declined within a few months.

Reduction of oxygen concentration to low levels in the root zone reduces shoot growth of white clover (Gradwell, 1969) but waterlogging does not affect waterlogging tolerant clovers similarly. Hoveland and Mikkelson (1967) found root yield unaffected in white and ladino clover, but reduced in strawberry and Persian clovers whereas manganese accumulated in all but strawberry clover and nitrogen concentration fell only in intermediate white clover. A tropism of strawberry clover to curve stems upward during flooding confers additional tolerance to flooding (Bendixen and Peterson, 1962).

Intermediate white clover is more tolerant to flooding than several annual clover species (Hoveland and Webster, 1965). Specific differences in tolerance to waterlogging occur in the genus *Vicia* (Hoveland and Donnelly, 1966) and similarly between annual *Medicago* species. The most tolerant species were *M. polymorpha*, *M. arabica* and *M. intertexta* and the most sensitive were *M. scutellata*, *M. tornata*, and *M. minima*. All annual medic species were more sensitive than subterranean clover to waterlogging (Francis and Poole, 1973).

2.5.2.2.2. Graminaceous species

Grass species generally are more tolerant to waterlogging than leguminous species. Examples of extreme tolerance under inundation are reported by Porterfield (1945) for Buffalo grass (*Buchloë dactyloides*) which survived submergence for nineteen months. Timothy (*Phleum pratense*) and reed canary grass (*Phalaris canariensis*) were not severely injured by 7 weeks inundation (Bolton and McKenzie, 1946). High tolerances for grasses have also been reported by Rhoades (1964) and Davis and Martin (1949).

Low oxygen flux into soil caused by excessive moisture and waterlogging differentially affect grass species. The more tolerant grasses produced thicker roots with less laterals and some less tolerant grasses produce a surface mat of roots in poorly aerated soil (Waddington and Baker, 1965). Other studies demonstrating the adaptation of species to a low but consistent soil oxygen flux have been done by Letey, Stolzy et al. (1964), Gradwell (1965, 1967) and West and Black (1969).

The tolerance of grasses to waterlogging and submersion is inversely related to the temperature in the root zone, however there are differences in tolerance between species particularly at lower temperatures (Beard and Martin, 1970).

Although grasses may tolerate flooding for long periods, Rogers and Davies (1973) found that under field conditions the yield and concentration of K,N, and Mg in the herbage of four grasses was positively correlated with soil oxygen levels and in a pot experiment a species X nutrient concentration interaction occurred demonstrating specific responses to flooding. Humphries (1962) described the differences in flooding tolerance between tolerant *Phalaris tuberosa* and intolerant *Ehrharta calycina*, however the former species exhibited an adverse reaction to flooding unless the nitrogen and phosphorus status of the soil was sufficiently high.

2.6. THE ECOLOGY OF LUCERNE

2.6.1. The taxonomy of *Medicago sativa* and its close relatives

Lucerne is the common name given in Australia to the species *Medicago sativa*. Cytogenetically this species is a member of a complex of taxa encompassing *Medicago sativa*, *M. falcata* and *M. glutinosa* and *M. coerulea* which are diploid forms of *M. falcata* and *M. sativa* respectively, (Gillies, 1972). In their review, Busbice, Hill and Carnahan (1972) concluded that segregation of alleles in lucerne is similar to that expected of an autotetraploid.

2.6.2. The distribution of lucerne in the world

Lucerne is a widely distributed pasture and fodder plant. (Klinkowski, 1933; Sinskaya, 1950; Bolton, 1962; Wilsie, 1962; Rogers, 1967; Bolton, Goplen and Baenziger, 1972). Its wild progenitors were distributed in Asia Minor, the Caucasian region and Central Asia, and from these centres it has been domesticated and cultivated in every major climatic zone except tropical and humid subtropical regions. A range of ecotypes has developed within this wide and diverse distribution. These ecotypes are usually categorized using an index of winterhardiness and earliness of resumption of growth in Spring (Bolton, 1962) or the allocation of varieties to regions of adaptation (Lowe, Marble and Rumbaugh, 1972).

2.6.3. The origin of lucerne varieties which are tolerant to poorly drained soil conditions

In the Morshansk region, near Tambov, U.S.S.R. natural hybrids between local wild yellow lucerne (*Medicago falcata*) and European lucerne (*M. sativa*) which was imported to the region, occur widely in the flood plains of the rivers Tsna and Kashma (Lubenets and Plotnikov, 1950). These authors described two varieties, 'Marusinskaya 81' and 'Marusinskaya 425'. Marusinskaya 81' is classified as a Central Russian violet-hybrid resistant to waterlogging. Marusinskaya 425 is described as a North Russian yellow flowered hybrid ecotype tolerant to waterlogging. Both varieties were derived by mass selection from the natural interspecific hybrid population at the Morshansk State Plant Breeding Station and both are winter-hardy, winter dormant and semi-procumbent in growth habit.

In North America two varieties 'Rhizoma' and 'Narragansett' have been reported to express tolerance to wet soil conditions.

'Rhizoma' lucerne was released in 1948 from a mass selection programme of six generations based on six hybrids resulting from natural crossing between two species; diploid *Medicago falcata* variety 'Don' imported from the U.S.S.R. and tetraploid *Medicago sativa* variety 'Grimm' and/or 'Ontario Variegated'. Don was the female parent and 'Rhizoma' is a tetraploid variety with 32 somatic chromosomes (Nilan, 1951).

Heinrichs (1968) reported that 'Rhizoma' is quite widely adapted in Canada and seems to be better able to withstand acid and imperfectly drained soils than most other varieties. He described 'Rhizoma' as a winter hardy variety, tending to develop very broad crowns from rhizomes. Its root system is mainly of the branched type, without a prominent taproot.

'Narragansett' lucerne released in 1946, was developed at the Rhode Island Agricultural Experiment Station from a wide range of genetic material including 'Grimm', 'Canadian Variegated', 'Hardigan', 'Cossack', 'Hansen', 'Ladak', and several strains of *Medicago falcata*. A major contribution in the synthesis of the variety was seed from the same natural interspecific cross used for the basis of 'Rhizoma' (Odland and Skogley, 1953). 'Narragansett' appears to be better suited to imperfectly drained acid soils than most other varieties. It is a winter-hardy, winter dormant variety with either a tap or branched root system (Heinrichs, 1968).

The four varieties for which tolerance to poorly drained soil conditions have been reported contain one common source within their diverse parentage, namely yellow-flowered wild-growing lucerne from a region in North and Central Russia.

A number of ecotypes of Medicago falcata have been described from this region and they are reported to occur often in river floodplains and adjacent floodlands (Sechkarev, 1950).

2.6.4. The productivity of lucerne ecotypes in Australia

The lucerne varieties which have been accepted commercially in Australia have been introduced from either mediterranean or warm temperate environments. In lucerne breeding in Australia selection has been against extreme winter dormancy (Register of Australian Herbage Plant Cultivars, 1972).

The hardy winter-dormant varieties of central Europe, Canada and northern U.S.A. are low yielding in early Spring and late Autumn and are generally much lower yielding than ecotypes from mediterranean and warm temperate regions (Rogers and Bailey, 1968; Leach, 1971).

If tolerance to waterlogging was to be found in the hardy winter-dormant varieties, then selection from a hybrid population resulting from crosses between these and the local varieties may provide an agronomically acceptable variety for some areas in Australia.

2.7. SOILS IN SOUTH AUSTRALIA WHICH ARE LIABLE TO WATERLOGGING

In South Australia the major soil types subject to waterlogging as a result of perched watertables are the solodized solonetz and groundwater rendzina soils in the lower southeast of the State (Blackburn, 1964) and podsolic and lateritic soils in the Adelaide Hills, Fleurieu Peninsula and on Kangaroo Island (Rix and Hutton, 1953; Northcote and Tucker, 1948). Small areas of lateritic podsols, grey heavy textured soils and solodized solonetz soils which become waterlogged occur in lower Eyre Peninsula (French, 1958). Areas of soils related to the South Australian duplex types (podsols and lateritic podsols) are present in the eastern states of Australia and Western Australia and on these winter waterlogging occurs in areas of relatively high rainfall.

3. EXPERIMENT 1: THE EFFECT OF WATERLOGGING ON THE GROWTH OF EIGHT LUCERNE VARIETIES ESTABLISHED IN THREE DIFFERENT SOILS

3.1. MATERIALS

3.1.1. Varieties

Eight lucerne varieties were chosen to encompass the range of waterlogging tolerance reported in the literature and to also include an extreme winter-active Mediterranean genotype.

The varieties and their origin were:

	VARIETY	ORIGIN
1.	Marusinskaya 81	Morshansk, U.S.S.R.
2.	Marusinskaya 425	Morshansk, U.S.S.R.
3.	Rhizoma	Canada
4.	Narragansett	U.S.A.
5.	Du Puits	Australia, ex France
6.	Hunter River	Australia
7.	African	Australia, ex Egypt
8.	Demnat	Australia, ex Morocco

Seed of the varieties 'Marusinskaya 81' and 'Marusinskaya 425' was obtained from the All-Union Institute of Plant Industry, Leningrad, U.S.S.R.; 'Rhizoma' seed was obtained from the Canada Department of Agriculture, Ottawa, Canada and 'Narragansett' from the Plant Introduction Section, U.S.D.A., Beltsville, Maryland, U.S.A.

Seed of the remaining varieties was produced in Australia from populations originating from the countries listed.

3.1.2. Soils

Three soils from areas susceptible to waterlogging during the winter period of intensive rainfall were used in this experiment.

3.1.2.1. Solodized Solonetz

The loamy sand horizons to a depth of 20 cm from a solodized solonetz soil profile on the Kybybolite Research Centre, South Australia were homogenized. The profile from which the soil was taken is described by Stace et al. (1968). Their description is attached (see Appendix 1).

3.1.2.2. Groundwater Rendzina

The second soil was the upper 20 cms from a groundwater rendzina situated approximately on the boundary of the Hynam and Maaoope associations described by Blackburn (1964). The profile was described by Clarke (1965) and his description is attached (Appendix 2).

3.1.2.3. Lateritic Podsol:

The third soil was the upper 20 cm from a lateritic podsol soil obtained from the Second Valley Forest, South Australia. The soil profile is very similar to those described as lateritic podsols by Raupach (1966) and a detailed analysis of a profile from the locality used to obtain the soil stock for this experiment was supplied by A.R.P. Clarke C.S.I.R.O., Div. of Soils, Adelaide (Personal communication). This description is also attached (Appendix 3).

Appendix 4 presents descriptive data for the profiles from which the soils were taken for this experiment. The percentage total soluble salts, the pH, and the mechanical analysis are presented for each morphologically or visionally distinct level within the profiles.

3.2. METHODS

The three soil types were placed in plastic pots 15 cm high and 15 cm in diameter. Fertilizer was mixed into the top 3 cm within each pot at the rates given in Table 2.

Seed of the eight varieties were germinated at 20°C on wet filter paper in petri dishes beginning on April 21, 1972. One week later five seedlings were planted per pot. The seedlings were allowed to establish for eight weeks with daily watering.

TABLE 2

Rates and forms of nutrients added to all soils used in Experiment 1.

NUTRIENT	FORM	RATE (K.h.$^{-1}$)
P	Superphosphate (Commercial)	200
K	KCL	200
Ca(Mg)	Ca CO_3 (Mg CO_3) (dolomitic	100
Cu	$CuSO_4$	3.5
Zn	$ZnSO_4$	2
Mo	$Na_2Mo_2O_4$	2
Co	$CoSO_4$	2

Rhizobial inoculum was applied as a water suspension during the first days after planting.

The plants were grown in a glasshouse equipped with reverse-cycle air conditioning and were maintained at or above 11°C. Artificial lighting was provided by nine 100 Watt incandescent lamps suspended 1.3 metres above the pots and automatically switched to provide a day length of 18 hours. This light intensity has been found sufficient to provide a day-length effect and to keep winter dormant plants growing actively, but it has little, if any, photosynthetic effect.

The daily minimum, mean and maximum temperature and humidity were recorded (Appendix 5).

The experimental design was two replicates of a complete factorial of eight varieties × three soils × two flooding treatments × four harvests with the 192 treatments placed randomly within each replicate.

The flooding treatment was a complete saturation of the pot of soil by standing it in a neatly fitting plastic bucket in which the water level was maintained just above the soil surface by daily addition to the plastic bucket. The alternate flooding treatment was a nonflooded freely drained control pot. The flooding treatment was commenced at the first harvest.

The harvesting schedule was:

<u>Harvest 1</u>: On June 23, 1972, eight weeks after seedlings were transplanted

<u>Harvest 2</u>: July 3, 1972, 10 days after flooding commenced

<u>Harvest 3</u>: July 13, 1972, 20 days after flooding commenced

<u>Harvest 4</u>: August 2, 1972, 40 days after flooding commenced

At each harvest the plants were gently washed free of soil and divided into top and root components by cutting at the point of intersection of the former soil surface. Plant tops and roots from all the plants in each pot were weighed to provide a fresh weight and then dried for 12 hours at 70°C and weighed.

The number of plants present in each pot at the commencement of flooding (Harvest 1) was recorded.

At harvest 1 the plants in pots which remained for subsequent harvests were cut back to five centimetres above the soil surface. The plants destructively sampled at Harvest 1 were divided into two top sections: lower tops being the lower 5 cms and upper tops being the growth above 5 cms in each pot. The lower tops were equivalent to the top remaining in all other pots after harvest 1.

At harvests 3 and 4 the number of plants which did not have any green coloration in the apex of the tallest stem, but which had become yellow, chlorotic or had died, were classified as'dead' but their growth was included with the remaining 'living' plants to obtain yield data.

3.3. RESULTS

3.3.1. The overall effect of flooding and soil type on plant growth

Flooding caused a severe reduction in the yield of both tops and roots of the lucerne plants (Tables 3a, 3b, 3c and 3d). The yields presented for the first harvest are of the lower tops portion which was equivalent to the plant retained at the commencement of flooding.

Flooding significantly reduced all yields after 10, 20 and 40 days except for the dry weight of tops at 10 days. Although the yields of the unflooded controls continued to increase, the yield of plant tops did not increase after 10 or 20 days of flooding and the yield of plant roots declined under waterlogged conditions.

Significant soil x flooding interactions only occurred for plant tops. The interactions were caused by the large and significant differences between soils in the non-flooded controls whereas in the flooded soils the overall response of varieties was similar. An analysis of differences in yields between soils within each of the flooding treatments demonstrated that yields in the non-flooded treatment were generally highest in the groundwater rendzina soil, intermediate in the solodized solonetz and lowest in the lateritic podsol.

TABLE 3a

The average fresh weight per plant top of all varieties at each harvest within soil and flooding treatments. (gm. per plant)

Flooding Comparison	Soil	Days of Flooding			
		0	10	20	40
Non flooded	Solodized Solonetz	1.42	2.09	3.13	4.65
	Groundwater Rendzina	1.28	2.92	4.00	6.41
	Lateritic Podsol	0.99	1.87	2.48	3.80
	Mean of Soils	1.23	2.29	3.20	4.95
Flooded	Solodized Solonetz	1.25	1.85	1.60	1.85
	Groundwater Rendzina	1.46	2.09	2.18	2.15
	Lateritic Podsol	0.99	1.82	1.78	2.08
	Mean of Soils	1.23	1.92	1.85	2.03
L.S.D.'s	Flooding v. Nonflooding				
	.05		.219	.249	.318
	.01	N.S.	.294	.333	.426
	.001		.384	.436	.558
	Soil x flooding				
	.05		.380	.431	.552
	.01	N.S.	.509	.572	.738
	.001		.666	.753	.966
	Soils within Nonflooded				
	.05	.261	.329	.523	.680
	.01	.355	.447	.711	.923
	.001	.476	.600	.953	1 .239
	Soils within Flooded				
	.05	.233		.362	
	.01	.316	N.S.	.492	N.S.
	.001	.424		.660	

TABLE 3b

The average dry weight per plant of plant tops of all varieties at each harvest within soil and flooding treatments. (gm. per plant)

Flooding Comparison	Soil	Days of Flooding			
		0	10	20	40
Non flooded	Solodized Solonetz	0.26	0.39	0.61	1.19
	Groundwater Rendzina	0.29	0.52	0.78	1.68
	Lateritic Podsol	0.17	0.32	0.46	0.98
	Mean of Soils	0.24	0.41	0.62	1.28
Flooded	Solodized Solonetz	0.23	0.37	0.42	0.47
	Groundwater Rendzina	0.30	0.43	0.55	0.55
	Lateritic Podsol	0.18	0.32	0.40	0.49
	Mean of Soils	0.24	0.37	0.46	0.51
L.S.D.'s	Flooding v. Nonflooding				
	.05	N.S.	N.S.	.056	.098
	.01			.075	.131
	.001			.099	.171
	Soil x flooding				
	.05	N.S.	N,S.	.097	.170
	.01			.130	.227
	.001			.170	.297
	Soils within Nonflooded				
	.05	.049	.054	.103	.211
	.01	.066	.073	.139	.286
	.001	.089	.098	.197	.384
	Soils within flooded				
	.05	.046	.129	.099	N.S.
	.01	.063	.175	.134	
	.001	.084	.235	.180	

TABLE 3c.

The average fresh weight per plant of plant roots of all varieties at each harvest within soil and flooding treatments. (gm. per plant)

Flooding Comparison	Soil	Days of Flooding			
		0	10	20	40
Non flooded	Solodized Solonetz	2.23	2.36	2.95	5.07
	Groundwater Rendzina	2.60	3.23	2.97	5.36
	Lateritic Podsol	2.59	2.77	3.26	5.70
	Mean of Soils	2.48	2.79	3.86	5.38
Flooded	Solodized Solonetz	1.85	2.13	1.81	1.40
	Groundwater Rendzina	2.80	2.40	1.67	1.15
	Lateritic Podsol	2.73	2.35	2.16	1.94
	Mean of Soils	2.46	2.29	1.88	1.50
L.S.D's.	Flooding v. Nonflooding				
	.05	N.S.	.384	.368	.509
	.01		.513	.493	.681
	.001		.671	.645	.891
	Soil x flooding				
	.05	N.S.	N.S.	N.S.	N.S.
	.01				
	.001				
	Soils within Nonflooded				
	.05	N.S.	.603	N.S.	N.S.
	.01		.818		
	.001		1.097		
	Soils within flooded				
	.05	.512	N.S.	N.S.	.347
	.01	.695			.471
	.001	.933			.631

TABLE 3d

The average dry weight per plant of plant roots of all varieties at each harvest within soil and flooding treatments. (gm. per plant)

Flooding Comparison	Soil	Days of Flooding			
		0	10	20	40
Non flooded	Solodized Solonetz	0.48	0.45	0.55	1.47
	Groundwater Rendzina	0.63	0.71	0.75	1.81
	Lateritic Podsol	0.44	0.48	0.55	1.63
	Mean of Soils	0.52	0.55	0.62	1.64
Flooded	Solodized Solonetz	0.36	0.35	0.31	0.25
	Groundwater Rendzina	0.68	0.59	0.45	0.30
	Lateritic Podsol	0.57	0.37	0.33	0.28
	Mean of Soils	0.53	0.44	0.37	0.28
L.S.D's.	Flooding v. Nonflooding				
	.05	N.S.	.069	.058	.167
	.01		.093	.078	.224
	.001		.122	.102	.293
	Soil x flooding				
	.05	N.S.	N.S.	N.S.	N.S.
	.01				
	.001				
	Soils within nonflooded				
	.05	.157	.103	.098	N.S.
	.01	.213	.139	.132	
	.001	.285	.187	.178	
	Soils within flooded				
	.05	.189	.132	.112	N.S.
	.01	.257	.179	.152	
	.001	.345	.240	.204	

3.3.2. The effect of the flooding treatments and the soils upon the growth of the eight lucerne varieties

Although the overall effect of flooding was a reduction of the yield of tops and roots of lucerne, significantly different responses of the varieties occurred in both the non-flooded and flooded treatments (Tables 4a, 4b, 4c and 4d).

3.3.2.1. Growth in the non-flooded treatment

At harvest 1, when the differential flooding treatments were commenced, there was no significant difference between the two flooding treatments and the yields from each treatment were combined and analysed for differences between varieties. To allow comparisons between the four harvests only the yields of the lower tops at harvest 1 are included in Tables 4a and 4b. In harvest 1 there were few differences between the yields of the lower tops and roots of the varieties. The significantly higher average plant yields of 'Rhizoma' and 'Du Puits' are a reflection of the low number of plants which established per pot (2.67 and 3.92 respectively compared with an overall average of 4.05).

In data for the total yield per pot (not presented) plant density caused significantly lower yields for these two varieties but the pattern of performance of all other varieties was similar to that of the average yield per plant as presented.

The total herbage yields per plant at harvest 1 (Table 5) show that the yields of the varieties were similar (the effect of plant numbers is again evident for 'Rhizoma' and 'Du Puits') and in the three subsequent harvests there was not a consistent intervarietal pattern of yield and after forty days there were no significant differences between varieties for any yield component (Tables 4a, 4b, 4c and 4d).

A consistent population x soil interaction for the average yield of plant tops per plant was caused by the significantly lower yields of some varieties in the groundwater rendzina soil (Tables 5 and 6).

TABLE 4a

The average fresh weight of plant tops of each variety averaged over all soils within the flooded treatments.(gm. per plant)

	Days from Harvest 1						
Population	0	10		20		40	
		N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	1.34	2.26	2.51	3.73	2.23	4.97	2.99
Marusinskaya 425	1.35	2.48	1.40	2.63	1.95	4.21	2.83
Rhizoma	1.52	2.00	2.15	2.97	1.56	5.03	1.78
Narragansett	1.30	2.28	1.92	3.04	2.62	4.99	1.87
Du Puits	1.42	2.65	2.11	4.21	1.85	5.46	2.76
Hunter River	1.19	1.92	1.88	2.86	1.75	4.92	1.35
African	0.96	2.44	1.92	2.86	1.39	4.64	1.52
Demnat	0.99	2.31	1.44	3.32	1.47	5.38	1.12
Mean of Populations	1.23	2.29	1.92	3.20	1.85	4.95	2.03
L.S.D.'s Population							
.05	.275		.661	.855	.591		.664
.01	.368	N.S.	.898	1.160	.803	N.S.	.902
.001	.481		1.204	1.556	1.077		1.210
Population x flooding							
.05		.621		.708		.900	
.01	N.S.	.831		.947		1.205	
.001		1.087		1.239		1.577	

TABLE 4b

The average dry weight of plant tops of each variety averaged over all soils within the flooded treatments.(gm. per plant)

	Days from Harvest 1						
		10		20		40	
Population	0	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	0.23	0.38	0.52	0.74	0.57	1.13	0.57
Marusinskaya 425	0.23	0.43	0.27	0.45	0.46	1.00	0.55
Rhizoma	0.30	0.42	0.44	0.55	0.38	1.22	0.53
Narragansett	0.24	0.41	0.39	0.53	0.61	1.34	0.60
Du Puits	0.28	0.45	0.43	0.83	0.46	1.31	0.55
Hunter River	0.23	0.36	0.38	0.58	0.39	1.35	0.41
African	0.21	0.41	0.33	0.55	0.33	1.38	0.47
Demnat	0.22	0.44	0.24	0.72	0.44	1.55	0.37
Mean of Populations	0.24	0.41	0.37	0.62	0.46	1.28	0.51
L.S.D.'s.							
Population							
.05	.053	N.S.	.129	.167	.161	N.S.	N.S.
.01	.071		.175	.227	.219		
.001	.092		.235	.304	.294		
Population x flooding							
.05	N.S.	.119		.159		.277	
.01		.159		.212		.371	
.001		.208		.278		.485	

TABLE 4c

The average fresh weight of plant roots of each variety averaged over all soils within the flooding treatments. (gm. per plant)

Population	Days from Harvest 1						
	0	10		20		40	
		N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	2.15	2.16	1.95	3.62	1.32	6.26	0.88
Marusinskaya 425	2.18	2.75	1.27	2.96	1.62	4.95	1.78
Rhizoma	2.41	2.57	2.14	2.88	1.21	4.81	0.98
Narragansett	2.29	3.00	2.07	3.33	3.00	5.32	1.32
Du Puits	3.36	4.13	3.47	3.37	2.30	6.34	2.50
Hunter River	2.33	2.30	2.83	2.63	1.70	4.98	1.02
African	2.38	3.61	2.96	3.19	1.87	4.41	1.37
Demnat	2.65	1.75	1.66	2.49	2.02	5.94	2.11
Mean of Populations	2.47	2.79	2.29	3.86	1.80	5.38	1.50
L.S.D.'s.							
Population							
.05	.705	.984	1.115		.983		.566
.01	.944	1.335	1.513	N.S.	1.335	N.S.	.769
.001	1.235	1.791	2.030		1.790		1.031
Population x flooding							
.05							
.01	N.S.	N.S.		N.S.		N.S.	
.001							

TABLE 4d

The average dry weight of plant roots of each variety averaged over all soils within the flooding treatments. (gm. per plant)

	Days from Harvest 1						
Population	0	10		20		40	
		N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	0.41	0.40	0.34	0.74	0.28	2.31	0.25
Marusinskaya 425	0.40	0.51	0.26	0.52	0.23	1.28	0.23
Rhizoma	0.59	0.47	0.46	0.57	0.25	1.36	0.23
Narragansett	0.50	0.59	0.49	0.64	0.41	1.48	0.27
Du Puits	0.67	0.78	0.57	0.75	0.49	1.70	0.40
Hunter River	0.49	0.56	0.49	0.48	0.35	1.69	0.23
African	0.50	0.64	0.53	0.61	0.41	1.42	0.27
Demnat	0.62	0.44	0.37	0.62	0.47	1.88	0.35
Mean of Populations	0.52	0.55	0.44	0.62	0.36	1.64	0.28
L.S.D.'s Population							
.05		.167		.159	.183		.100
.01	N.S.	.227	N.S.	.216	.248	N.S.	.135
.001		.305		.290	.333		.181
Population x flooding							
.05							
.01	N.S.	N.S.		N.S.		N.S.	
.001							

TABLE 5.

The average dry weight per plant of the total plant tops at Harvest 1. (gm. per plant).

Population	Soil			
	Solodized Solonetz	Groundwater Rendzina	Lateritic Podsol	Population Mean
Marusinskaya 81	0.35	0.53	0.36	0.42
Marusinskaya 425	0.31	0.61	0.21	0.38
Rhizoma	0.48	1.10	0.23	0.60
Narragansett	0.28	0.72	0.19	0.40
Du Puits	0.45	0.66	0.38	0.49
Hunter River	0.29	0.64	0.21	0.38
African	0.33	0.67	0.39	0.46
Demnat	0.48	0.83	0.25	0.52
Means	0.37	0.72	0.28	0.46

L.S.D.'s.	Population	Soil	Population x Soil
.05	0.118	0.072	0.204
.01	0.158	0.097	0.274
.001	0.207	0.126	0.358

TABLE 6.

The average dry weight per plant of plant tops at Harvest 4 in the nonflooded treatment. (gm.)

Population	Soil Solodized Solonetz	 Groundwater Rendzina	 lateritic Podsol	Population Mean
Marusinskaya 81	1.23	1.13	1.03	1.13
Marusinskaya 425	0.83	0.88	1.29	1.00
Rhizoma	1.03	1.81	0.83	1.22
Narragansett	1.14	1.86	1.02	1.34
Du Puits	1.39	1.66	0.87	1.31
Hunter River	1.24	1.67	1.15	1.35
African	1.13	2.25	0.75	1.38
Demnat	1.50	2.21	0.93	1.55
Means	1.19	1.68	0.98	1.28

L.S.D.'s.	Population	Soil	Population x Soil
.05		0.211	0.596
.01	N.S.	0.286	0.810
.001		0.384	1.086

After forty days regrowth all varieties other than 'Marusinskaya 81' and 'Marusinskaya 425' expressed higher yields in the groundwater rendzina soil, but there were no overall differences (Table 6).

The root yields of varieties were similar before flooding commenced and few significant differences occurred at subsequent harvests and after forty days there were no intervarietal differences in the yield of roots per plant (Tables 4c and 4d). Although some significant overall differences in root yields had occurred between soils (Tables 3c and 3d) there were no significant population x soil interactions (data not presented) corresponding to those for herbage yields.

3.3.2.2. Growth in the flooded treatment

In harvests at ten, twenty and forty days after the commencement of flooding the most consistent varietal pattern of top growth was for 'Hunter River', 'African' and 'Demnat' to be lower yielding and the remaining varieties, particularly 'Marusinskaya 81' to be higher yielding (Tables 4a and 4b). The pattern of root yields (Tables 4c and 4d) was variable from harvest to harvest and did not consistently relate to the yields of the tops. Unlike the yields of tops, root yields did not increase after the imposition of flooding and the variation in yield reflects the variation in expression of resistance to root rotting organisms and the production of some weak adventitious surface root systems by individual plants.

Population x flooding interactions were only significant in the yield of tops and generally resulted from the sensitivity of the varieties 'Hunter River', 'African' and 'Demnat', relative to the less affected varieties, 'Marusinskaya 81', 'Marusinskaya 425', 'Rhizoma' and 'Narragansett'. The results for the variety 'Du Puits' were more variable and its performance is intermediate between the four more tolerant and the remaining three most sensitive varieties (Tables 4a and 4b).

The relative yields of the varieties under flooding and the significant population x flooding interactions provide evidence of variation in tolerance to waterlogging between the eight varieties in which the group of four introduced varieties is more tolerant than the four Australian varieties.

In the flooded treatment there were no significant population x soil interactions for either top or root yield (data not presented).

3.3.3. The effect of flooding upon the dry weight: fresh weight ratio in plant tops and roots

3.3.3.1. Plant tops

Flooding increased the ratio of dry weight to fresh weight in plant tops after ten and twenty days of flooding relative to the non-flooded treatment (Table 7). After forty days the ratio had risen in the non-flooded control plants because of the higher proportion of stem tissue in the tops and there was no significant difference between the flooding treatments.

The effect of flooding within and between varieties was most marked after twenty days when all varieties but 'Hunter River' had a higher ratio of dry to fresh weights in the flooded treatment than in the non-flooded (Table 8). In the non-flooded treatment the leafier varieties 'Marusinskaya 425', 'Rhizoma' and 'Narragansett' tended to have lower ratios and within the flooded treatment all varieties were similar except 'Demnat' which had a significantly higher ratio than most varieties, thereby expressing an extreme sensitivity to flooding.

A significant soil x flooding interaction occurred after twenty days of flooding caused by a lower ratio in the lateritic podsol soil, but generally there were no significant differences between soils in response of the dry weight to fresh weight ratio of plant tops.

3.3.3.2. Roots

The ratio of dry to fresh weight of plant roots was not significantly

TABLE 7.

The effect of flooding and soil on the ratio of dry weight to fresh weight at four harvests.

Flooding Comparison	Soil	Days from Harvest 1			
		0	10	20	40
Non flooded	Solodized Solonetz	0.183	0.190	0.196	0.257
	Groundwater Rendzina	0.223	0.179	0.195	0.258
	Lateritic Podsol	0.169	0.176	0.188	0.262
	Mean of soils	0.189	0.182	0.193	0.259
Flooded	Solodized Solonetz	0.179	0.200	0.268	0.303
	Groundwater Rendzina	0.207	0.206	0.254	0.264
	Lateritic Podsol	0.176	0.175	0.222	0.260
	Mean of Soils	0.189	0.194	0.248	0.276
L.S.D.'s.	Flooding v. Nonflooding				
	.05	N.S.	0.010	0.010	N.S.
	.01		0.013	0.014	
	.001		0.017	0.018	
	Soil x Flooding				
	.05	N.S.	N.S.	0.013	N.S.
	.01			0.024	
	.001			0.036	

TABLE 8

The ratio of dry weight to fresh weight of plant tops of each variety averaged over all soils within flooding treatments.

	Days from Harvest 1						
Population	0	10		20		40	
		N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	.173	.168	.210	.201	.249	.226	.192
Marusinskaya 425	.169	.174	.187	.171	.232	.236	.189
Rhizoma	.193	.208	.202	.186	.237	.241	.306
Narragansett	.181	.179	.201	.173	.239	.272	.320
Du Puits	.197	.172	.209	.196	.253	.241	.202
Hunter River	.185	.191	.200	.205	.221	.278	.298
African	.206	.167	.178	.194	.241	.290	.313
Demnat	.212	.196	.162	.217	.312	.286	.383
Mean of Populations	.189	.182	.194	.193	.248	.259	.276
L.S.D.'s.							
Population							
.05	.018						
.01	.024	-		-		-	
.001							
Flooding							
.05		.010		.010			
.01	N.S.	.013		.014		N.S.	
.001		.017		.018			
Population x flooding							
.05		.028		.029			
.01	N.S.	.037		.039		N.S.	
.001		.048		.051			

affected by flooding until forty days after submergence, when the ratio was lower in the flooded treatment (Table 9), but there were no significant population x flooding or soil x flooding interactions. In the groundwater rendzina soil the roots were less affected by flooding (Table 3d) and contained less spongy soft necrotic tissue with a high water content thereby causing a significantly higher ratio in that soil (Table 9).

3.3.4. The effect of flooding upon the proportion of plants retaining active apical meristems

When lucerne plants are flooded, most become pale in appearance and depending upon their tolerance to waterlogging, the duration of waterlogging and soil type, the apical meristemmatic activity may cease. The cessation is evident from the lack of new leaves.

The loss of meristemmatic activity was least in the varieties 'Marusinskaya 81', 'Marusinskaya 425', 'Rhizoma' and 'Narragansett', intermediate in 'Du Puits', and greatest in 'Hunter River', 'African', and 'Demnat', which was severely affected (Table 10). Using this index, the proportion of tolerant plants was significantly lower in the solodized solonetz soil. The differences in appearance between varieties under flooded and non-flooded conditions in the three soils are illustrated in Figures 1 to 6. Although the population x soil interaction was not significant (Table 10) two anomolous varietal effects may have occurred: 'Rhizoma' was severely affected in the solodized solonetz soil and many 'African' plants did not cease meristemmatic activity or lose green coloration in the lateritic podsol soil (Fig. 6).

3.4. DISCUSSION AND CONCLUSIONS

The overall effect of flooding on lucerne was severe, but there were significant differences between the eight varieties included in this experiment which could be classified into a more tolerant group containing the introduced varieties 'Marusinskaya 81', 'Marusinskaya 425', 'Rhizoma'

TABLE 9.

The ratio of dry weight to fresh weight of roots at Harvest 4.

Population	Soil						Population Mean	
	Solodized Solonetz		Rendzina		Lateritic Podsol			
	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Marusinskaya 81	.321	.303	.308	.367	.424	.221	.351	.297
Marusinskaya 425	.309	.144	.271	.165	.214	.097	.265	.135
Rhizoma	.334	.216	.323	.247	.229	.212	.295	.225
Narragansett	.250	.189	.321	.314	.275	.180	.282	.228
Du Puits	.240	.240	.323	.262	.238	.111	.267	.204
Hunter River	.324	.211	.315	.269	.402	.206	.347	.229
African	.287	.199	.439	.224	.189	.182	.305	.202
Demnat	.301	.117	.398	.322	.263	.138	.320	.192
Flooding Mean	.296	.202	.337	.271	.279	.168	.304	.214
Soil Mean	.249		.304		.224		.259	

L.S.D.'s	Soil	Flooding	Popn x Flooding	Soil x Flooding
.05	.022	.018		
.01	.030	.024	N.S.	N.S.
.001	.039	.032		

TABLE 10.

The proportion of plants within the flooded treatments which retained apical meristemmatic activity after 40 days of flooding.

Population	Soil			
	Solodized Solonetz	Groundwater Rendzina	Lateritic Podsol	Population Mean
Marusinskaya 81	0.70	1.00	0.75	0.82
Marusinskaya 425	1.00	1.00	1.00	1.00
Rhizoma	0.35	1.00	1.00	0.78
Narragansett	1.00	0.80	1.00	0.93
Du Puits	0.50	1.00	0.75	0.75
Hunter River	0.13	0.40	0.60	0.38
African	0.10	0.10	0.75	0.32
Demnat	0.10	0.10	0.10	0.10
Means	0.48	0.68	0.74	0.63

L.S.D.'s.	Population	Soil	Population × Soil
.05	0.323	0.198	N.S.
.01	0.438	0.268	
.001	0.588	0.360	

FIGURE 1.

A representative plant from each lucerne variety taken from the nonflooded treatment in the solodized solonetz soil after 40 days of growth.

FIGURE 2.

A representative plant from each lucerne variety taken from the flooded treatment in the solodized solonetz soil after 40 days of flooding.

Abbreviations for the Names of Varieties in Figs. 1 to 6.

M81	Marusinskaya 81
M425	Marusinskaya 425
R	Rhizoma
N	Narragansett
DP	Du Puits
HR	Hunter River
A	African
D	Demnat

FIGURE 1.

FIGURE 2.

FIGURE 3.

A representative plant from each lucerne variety taken from the nonflooded treatment in the groundwater rendzina soil after 40 days of growth.

FIGURE 4.

A representative plant from each lucerne variety taken from the flooded treatment in the groundwater rendzina soil after 40 days of flooding.

FIGURE 3.

FIGURE 4.

FIGURE 5.

A representative plant from each lucerne variety taken from the nonflooded treatment in the lateritic podsolic soil after 40 days of growth.

FIGURE 6.

A representative plant from each lucerne variety taken from the flooded treatment in the lateritic podsolic soil after 40 days of flooding.

FIGURE 5.

FIGURE 6.

and 'Narragansett', and a less tolerant group containing the varieties 'Hunter River', 'African' and 'Demnat'. The performance of 'Du Puits' was intermediate between the two groups.

These eight varieties encompass the range of winter growth activities expressed by lucerne, from extreme winter dormancy of the Russian varieties to the active winter growth of 'Demnat' (Rogers and Bailey, 1968) but under the conditions of temperature and daylength used in this experiment all varieties had similar yields during establishment and in the nonflooded treatment, but in contrast in the flooding treatment, yield differences were expressed although growth was generally suppressed by flooding after ten to twenty days.

Because the plants were actively growing, the tolerance of the introduced winter dormant varieties could not be attributed to their dormancy, which could be an escape mechanism, but must be attributed to adaptive processes operative in actively growing plants.

Most plants in the four introduced varieties continued to develop leaves slowly and did not lose meristemmatic activity although growth was restricted by flooding after twenty days. In the ground-water rendzina soil the activity of these varieties was maintained for three or four weeks with little yellowing or senescence of leaves.

The varieties which did not maintain meristemmatic activity tended to yellow at the apices and subsequently leaf senescence and death of shoots occurred. The reduction of meristemmatic activity in the sensitive varieties was associated with significantly lower yields under flooding and the depression of yield by flooding in those varieties caused a significant variety x flooding interaction for the yield of top growth.

Although differences in yield and meristemmatic activity indicate the relative tolerance of varieties, the response of the roots to immersion is a critical factor.

After flooding there was no increase in total root mass, but it was observed that the root systems of some plants, particularly in the varieties which retained high meristemmatic activity, developed as a network of short thick sparsely branched roots or a mat of fine fibrous roots arising from near the plant crown ten or twenty days after flooding. Similar root development in wet soil has been reported by Tovey (1964) and Fox and Lipps (1955). The delay after flooding before establishment of these adventitious root systems has been reported in other species (Varade et al., 1970; Jackson, 1955).

Simultaneous with the development of compensatory root growth, rotting and disintegration of the deeper roots, taproots and crowns occurred at various rates and few plants retained a major proportion of the root mass present before flooding. The loss of functional root tissue may have caused moisture stress and an increase in the dry weight to fresh weight ratio in herbage.

In non-flooded conditions growth was highest in the groundwater rendzina soil, intermediate in the solodized solonetz and lowest in the lateritic podsol. Flooding reduced the differences between soils but adaptation to flooding was better in the groundwater rendzina than in the other soils (Tables 3a, b,c,d). There was no significant soil x population effect and the pattern of varietal performance was similar in all soils.

This experiment contained only two replicates and resolution of small effects was difficult, but the major effects of flooding, variety soil type and duration of flooding were demonstrated.

Within the Medicago and Trifolium inter- and intraspecific differences in waterlogging tolerance have also been reported (Francis and Poole, 1973; Francis and Devitt, 1969; Marshall and Millington, 1967). In this experiment variation in tolerance has been found within lucerne (Medicago sativa) but it is associated with winter dormant varieties and not strongly expressed in the four varieties registered for their agronomic suitability to southern Australia.

4. EXPERIMENT 2: THE EFFECT OF FLOODING IN THREE SOILS ON THE GROWTH OF HYBRID LUCERNE POPULATIONS DERIVED FROM CROSSES BETWEEN TOLERANT AND NON-TOLERANT VARIETIES

4.1. PRODUCTION OF HYBRID POPULATIONS

The eight varietal populations studied in Experiment 1 were used as parents to develop hybrid populations between the four varieties most tolerant to flooding (Marusinskaya 81, Marusinskaya 425, Rhizoma and Narragansett) and the four less tolerant varieties (Du Puits, Hunter River, African and Demnat).

The crosses which were made are set out in Table 11. It was considered important to study these combinations because the agronomic characteristics of the tolerant varieties are not suitable for southern Australia and the intolerant varieties are frequently killed where excessively most soil conditions occur for more than a few days. The remaining twenty four crosses to complete the diallel of eight parents were not included as they would have duplicated the parental types with their respective faults and would have considerably increased the size of the experiment.

Thirty plants of each parental variety were established in a glasshouse and crosses were made between randomly chosen plants of each variety. The flowers on female parents were not emasculated. Pollination was done manually using a folded piece of cartridge paper to trip the flowers of the male parent to collect pollen and then to trip and pollinate the female flower. (Previous experience has shown that self-pollination was a rare event using this crossing technique as plants which readily self-pollinate or self trip have not been detected.) Twenty to thirty racemes were pollinated per cross to produce the seed required. Seed for the eight parental populations was obtained from the same sources as in Experiment 1.

TABLE 11.

Hybrid and Parental Populations studied in Experiment 2.

Male Parent Female Parent	Marusinskaya 81	Marusinskaya 425	Rhizoma	Narragansett	Du Puits	Hunter River	African	Demnat
Marusinskaya 81	M81				M81 × DP	M81 × HR	M81 × A	M81 × D
Marusinskaya 425		M425			M425 × DP	M425 × HR	M425 × A	M425 × D
Rhizoma			R		R × DP	R × HR	R × A	R × D
Narragansett				N	N × DP	N × HR	N × A	N × D
Du Puits	DP × M81	DP × M425	DP × R	DP × N	DP			
Hunter River	HR × M425	HR × M425	HR × R	HR × N		HR		
African	A × M81	A × M425	A × R	A × N			A	
Demnat	D × M81	D × M425	D × R	D × N				D

4.2. EXPERIMENTAL DESIGN AND METHODS

The eight parental and thirty two hybrid populations were sown in a pot experiment in a glass house in the same soils and using the same flooding treatments as in Experiment 1. The forty populations were placed randomly within each of the six sub-blocks of soil X flooding treatments in each replicate. There were three replicates.

Seed was germinated on January 15, 1974 and ten seedlings were planted per pot on January 22 to 24. Fertilizer and inoculum were added and the plants were grown under freely drained soil conditions for eight weeks until the first harvest on March 20, when the flooding treatment was imposed. The harvest dates, measurements and observations which were made are:

DATE	PROCEEDURE/OBSERVATION/MEASUREMENT
March 20	Harvest 1: Dry weight of plant tops per pot Number of shoots per pot Number of plants per pot The flooding treatment was commenced
April 3	Score for plant appearance (after 14 days of flooding)
April 17	Score for plant appearance (after 28 days of flooding)
April 24	Score for plant appearance (after 35 days of flooding)
May 1	Harvest 2: Same measurements as in Harvest 1 The flooding treatment was removed
June 12	Harvest 3: Same measurements as in Harvest 1

The harvests were non-destructive and approximately 4 to 5 centimetres of growth were left above the crown at each harvest. The scores for plant appearance were made using a system from 1 to 9, 1 being a healthy plant showing no effect of flooding (non-flooded controls) and 9 a plant which appeared dead. The appearance of pots of plants used as standards are presented in Figs 7,8 and 9. Key indicators for rating plants at the scores were:

SCORE	INDICATOR
1	Healthy
2	Healthy with slightly lighter apices
3	Whole plant lighter in appearance
4	Yellowing of apices
5	Yellowing of apices and senesence of older leaves
6	No apical leaf production evident
7	Apices dead; some growth from crown buds
8	Growth from crown buds chlorotic and yellow
9	Plants appeared dead

Because of variation in the scores of individual plants in each pot the "mean appearance" was used as the score for the analyses. At harvest 2, plants which received a score of 5 or less were considered to have active meristems. After flooding was terminated plants which produced at least one new shoot were scored as plants which had regrown. At each harvest the number of shoots was taken as the number of stems severed by cutting off the top growth 5 cms above the crown.

The photoperiod was maintained at 18 hours or greater throughout the experiment by incandescent lights and minimum, mean and maximum temperatures and humidity are presented in Appendix 6.

4.3. RESULTS AND DISCUSSION

4.3.1. The overall effects of flooding and soil type on the average dry weight and the number of shoots per plant

Flooding again had a severe effect upon the growth of the lucerne populations. There was a severe reduction in the average yield and average number of shoots per plant when the flooding was compared with the non-flooded treatment (Tables 12 and 13).

FIGURE 7, 8 AND 9.

Pots of plants representative of each of the scores given for plant appearance during flooding in Experiments 2 and 3.

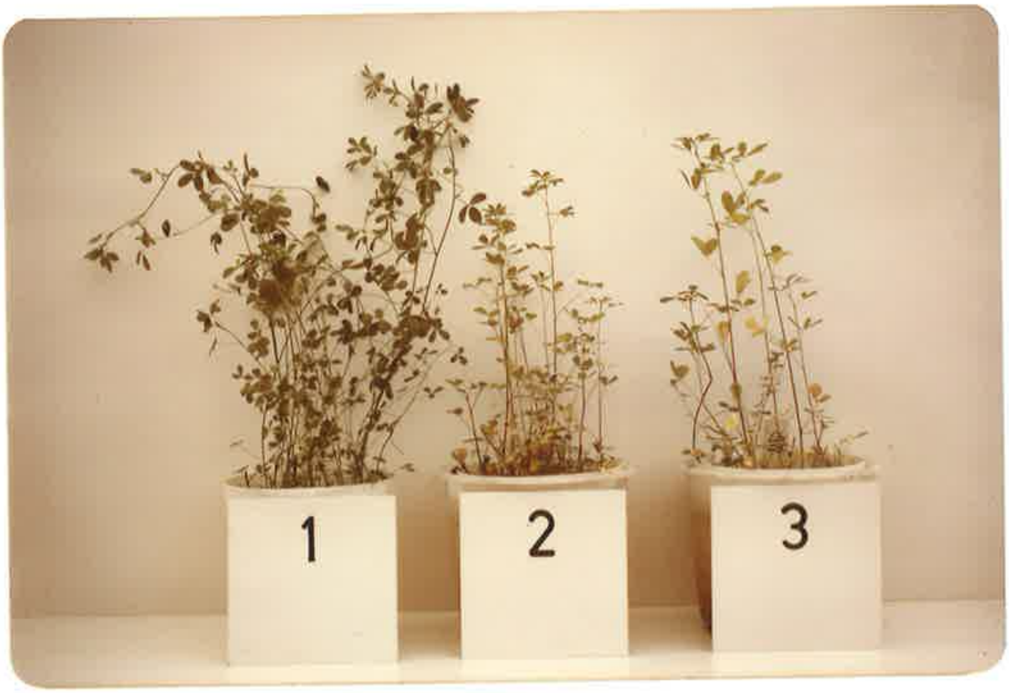


FIGURE 7.

FIGURE 8.

FIGURE 9.

TABLE 12.

The average dry weight of herbage per plant at each harvest.

(gm. per plant)

Harvest	Soil						Mean of all Soils	
	Solodized Solonetz		Groundwater Rendzina		Lateritic Podsol			
	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Harvest 1	0.220	0.230	0.374	0.409	0.124	0.125	0.239	0.254
Harvest 2	0.371	0.032	0.473	0.082	0.157	0.038	0.334	0.051
Harvest 3	0.359	0.048	0.561	0.195	0.166	0.036	0.362	0.093
Harvest 3/1	0.357	0.024	0.549	0.158	0.167	0.027	0.358	0.069

L.S.D.'s.	Flooding	Soil x Flooding
Harvest 1		
.05	N.S.	N.S.
.01		
.001		
Harvest 2		
.05	0.037	0.064
.01	0.052	0.091
.001	0.076	0.132
Harvest 3		
.05	0.067	0.116
.01	0.095	0.164
.001	0.137	0.238
Harvest 3/1		
.05	0.182	0.315
.01	0.259	0.448
.001	0.375	0.649

TABLE 13.

The average number of shoots per plant at each harvest.

Harvest	Soil						Mean of all Soils	
	Solodized Solonetz		Groundwater Rendzina		Lateritic Podsol			
	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
Harvest 1	1.84	1.87	2.22	2.36	1.19	1.14	1.75	1.79
Harvest 2	2.45	0.97	2.68	1.29	1.60	0.90	2.24	1.05
Harvest 3	2.45	1.17	2.90	1.88	1.73	0.87	2.36	1.31
Harvest 3/1	2.43	0.63	2.85	1.58	1.73	0.66	2.34	0.96

L.S.D.'s.	Flooding	Soil x Flooding
Harvest 1		
.05	N.S.	N.S.
.01		
.001		
Harvest 2		
.05	0.223	0.386
.01	0.317	0.549
.001	0.459	0.796
Harvest 3		
.05	0.143	N.S.
.01	0.204	
.001	0.295	
Harvest 3/1		
.05	0.182	0.315
.01	0.259	0.448
.001	0.375	0.649

During regrowth the effect of flooding persisted in all soils. Because flooding killed some plants the average yields and shoot numbers calculated after regrowth used the number of plants present before flooding to derive the data for harvests designated Harvest 3/1 in Tables 12,13, 14 and 15. The averages calculated after regrowth using the original number of plants were designated Harvest 3 in the same tables.

In the non-flooded treatment the yield was generally highest in the groundwater rendzina soil, intermediate in the solodized solonetz and lowest in the lateritic podsol. However the number of shoots was similar in the rendzina and solonetzic soil and lowest in the lateritic podsol.

The yields and shoot numbers per plant during establishment (harvest 1) were significantly correlated with those for subsequent harvests in the flooded treatments ($P < .001$). The data from harvests 2 and 3 were adjusted using the regression of each harvest on harvest 1. The actual values and adjusted values for yield and number of shoots, calculated using an analysis of covariance, are presented for the flooded treatment in Tables 14 and 15.

The adjusted values in the lateritic podsolic soil treatment were greater but not significantly higher than in the solodized solonetz soil. The average plant yields were consistently higher in the groundwater rendzina soil at each harvest. The average number of shoots per plant was higher during establishment and regrowth in the groundwater rendzina soil (harvests 1, 3 and 3/1) but flooding (harvest 2) eliminated differences in shoot production between the three soils.

4.3.2. The overall effect of flooding and soil type upon the appearance of lucerne plants

4.3.2.1. Scores for plant appearance

The overall effect of flooding was a decline in plant appearance relative to the unaffected healthy controls. The health of the plants declined as flooding proceeded; the rate of decline differed between soils (Table 16).

TABLE 14.

Actual and adjusted values for the average dry weight of herbage per plant within the flooded treatment. (gm. per plant)

Harvest	Actual Average Yield			Adjusted Average Yield		
	Soil			Soil		
	Solodized Solonetz	Rendzina	Lateritic Podsol	Solodized Solonetz	Rendzina	Lateritic Podsol
1	.230	.409	.125	-	-	-
2	.032	.082	.038	.034	.070	.048
3	.047	.195	.036	.052	.169	.058
3/1	.024	.158	.027	.026	.141	.041

L.S.D.'s.	For actual values			For adjusted values		
Harvest	.05	.01	.001	.05	.01	.001
1	.064	.106	.198	-	-	-
2	.023	.038	.071	.021	.035	.065
3	.058	.096	.180	.056	.093	.174
3/1	.049	.080	.150	.046	.076	.143

TABLE 15.

Actual and adjusted values for the average number of shoots per plant within the flooded treatment.

Harvest	Actual number of shoots.			Adjusted No. of shoots		
	Soil			Soil		
	Solodized Solonetz	Rendzina	Lateritic Podsol	Solodized Solonetz	Rendzina	Lateritic Podsol
1	1.87	2.36	1.14	-	-	-
2	0.97	1.29	0.90	0.95	1.20	1.01
3	1.17	1.88	0.87	1.15	1.73	1.04
3/1	0.63	1.57	0.66	0.61	1.42	0.83

L.S.D.'s.	For actual values			For adjusted values		
Harvest	.05	.01	.001	.05	.01	.001
1	.25	.41	.77	-	-	-
2		N.S.			N.S.	
3	.31	.51	.95	.28	.47	.88
3/1	.48	.79	1.48	.45	.75	1.40

TABLE 16.

The average visual score of all populations within each soil at three times of scoring after the commencement of flooding.

Number of days of flooding	Soil			
	Solodized Solonetz	Groundwater Rendzina	Lateritic Podsol	Average Score
14	4.22	2.00	2.00	2.74
28	6.71	4.83	5.23	5.59
35	7.69	5.78	6.89	6.79

Table of L.S.D.'s for comparison between soils

Days of Flooding	.05	.01	.001
14	-	-	-
28	.72	1.19	2.23
35	.53	.88	1.65

The effect of flooding was most severe in the solodized solinetz soil and least in the groundwater rendzina, but after 35 days of flooding the overall effect was severe in all soils.

4.3.2.2. Proportion of plants active at the apical meristem

Flooding reduced the number of plants in each pot with active apical meristems. The ratio between the number of plants active after flooding and the number present before flooding demonstrates the severe overall effect upon meristemmatic activity (Table 17). A ratio between the number of plants which produced new shoots after flooding was terminated and the number of plants present before flooding is a similar measure of overall survival of lucerne (Table 17).

In the non-flooded treatment virtually all plants survived the experiment, but in the flooded treatment the loss of meristemmatic activity was severe and differed significantly between the three soils, being highest in the solodized solonetz and lowest in the groundwater rendzina. During regrowth many plants which had ceased meristemmatic activity while flooded produced new shoots and the ratio of those surviving increased, but the more severe effect of the solodized solonetz soil persisted.

4.3.3. The effect of flooding and soil type upon the growth of parental and hybrid populations

The overall effect of flooding was so severe that there was a pronounced discontinuity in the distribution of errors and therefore to evaluate differences at the population level the analyses of variance were calculated separately for the flooded and non-flooded treatments in harvests 2 and 3.

The forty populations may be considered as eight parents divided into two groups of four from which have been derived two reciprocal and orthogonal 4 x 4 groups of top crosses.

Camparisons were made:

a. between any two of the forty populations

b. between any parent and the mean of any group of four hybrids which

TABLE 17.

The ratio of the number of plants retaining meristemmatic activity after flooding and after regrowth to the number of plants present before flooding.

Ratio	Soil						Overall Means	
	Solodized Solonetz		Growndwater Rendzina		Lateritic Podsol			
	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.	N.Fl.	Fl.
After flooding / before flooding.	0.99	0.21	0.99	0.48	1.00	0.33	0.99	0.34
Regrowth / before flooding.	0.99	0.54	0.99	0.84	1.00	0.74	0.99	0.71

L.S.D.'s.

Comparison between	.05	.01	.001
Flooding (After/Before)	.042	.060	.087
Soil x Flood (After/Before)	.074	.105	.151
Flooded Soils (After/Before)	.138	.228	.427
Flooding (Regrowth/Before)	.058	.082	.119
Soil x Flood (Regrowth/Before)	.100	.142	.206
Flooded Soils (Regrowth/Before)	.176	.292	.546

have a parent common to all four hybrids as either a female or male

c. between the means of any two sets of four hybrids

d. between a parent and the mean of the group of eight hybrids derived from it

e. between the means of two groups of eight hybrids

f. between the means of the two reciprocal sets of sixteen hybrids

4.3.3.1. Growth of non-flooded control populations

Harvest 1 and the non-flooded controls in harvests 2 and 3 permitted an evaluation of the parental and hybrid populations under non-flooded conditions.

A changing pattern of relationships was expressed by the average yield per plant and the average number of shoots per plant at the three harvests.

At harvest 1 the yields of the parents and their hybrid progenies were similar, except for the lower yields of the two Russian varieties (Marusinskaya 81 and 425) (Table 18), but in harvests 2 and 3 many hybrid progenies were higher yielding than their parents (tables 19 and 20). Therefore, crossing a parent from one group of four varieties with the four varieties from the alternate group of parents caused a heterotic effect.

The yields of parents did not differ significantly in harvest 2 and 3 except for lower yields of 'Hunter River' and 'Demnat' in harvest 2 (Table 19). Similarly, there were few significant differences between the means of eight hybrids in all harvests, although the yields of progeny of 'Hunter River' and 'Marusinskaya 81' tended to be low in harvests 2 and 3 and the progeny of 'Marusinskaya 425' was low yielding in harvest 3. Conversely 'Narragansett' progeny were higher yielding in harvest 2 and 'African' progeny were in harvest 3. The high yield of 'Rhizoma' was a consequence of the low number of plants which established per pot (6.67) compared with the overall mean (8.91).

TABLE 18.

The average dry weight per plant of parents and hybrid progenies derived from each parent at Harvest 1. (gm. per plant)

Parent	Parent Yield	Average yield of hybrid progenies
M81	.171	.240
M425	.134	.247
R	.288	.263
N	.214	.278
DP	.201	.249
HR	.221	.248
A	.218	.273
D	.213	.258

L.S.D.'s	Parents	Hybrid Progenies	Parents x Hybrids
.05	.049	.025	.052
.01	.065	.033	.069
.001	.083	.042	.088

TABLE 19.

The average dry weight per plant of parents and hybrid progeny groups in the nonflooded treatment at Harvest 2. (gm. per plant)

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	.287	.328	.296	.312
M425	.331	.381	.316	.349
R	.430	.303	.378	.341
N	.262	.392	.405	.399
DP	.315	.332	.374	.353
HR	.251	.309	.324	.317
A	.265	.340	.367	.354
D	.230	.361	.339	.350

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.057	.074	.095
Means of 4 hybrids	.048	.053	.067
A Mean of 4 hybrids & any parent.	.063	.083	.107
Means of 8 hybrids.	.028	.037	.048
A Mean of 8 hybrids & any parent.	.060	.079	.101

TABLE 20.

The average dry weight per plant of parents and hybrid progeny groups in the nonflooded treatment at Harvest 3. (gm. per plant)

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	.292	.349	.331	.340
M425	.258	.379	.313	.346
R	.546	.374	.421	.398
N	.315	.439	.396	.418
DP	.311	.358	.392	.275
HR	.243	.327	.338	.333
A	.276	.383	.488	.436
D	.236	.393	.399	.396

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.083	.109	.140
Means of 4 hybrids	.059	.077	.099
A Mean of 4 hybrids and any parent.	.093	.122	.157
Means of 8 hybrids	.042	.055	.070
A Mean of 8 hybrids and any parent.	.088	.116	.149

This effect of low plant numbers only occurred in the 'Rhizoma' population and in data for yield per pot, which is not presented, the effect was expressed as a lower yield.

There were no differences between reciprocal groups of sixteen crosses but there were between three male and female groups in harvest 2 (M425, R, DP) and two in harvest 3 (M425, A). These differences do not have any consistent pattern and were possibly caused by the superior or inferior performance of some plants within one set of the hybrids.

Hybrid vigour in the number of shoots produced per plant was expressed in harvest 1 but not in harvests 2 and 3. This was the reverse of the yield pattern in the same harvests (Tables 21,22,23). In harvest 1 the hybrids had more shoots than the parents and there were generally no large differences within the hybrid or parental groups except for a lower number of shoots in 'Marusinskaya 425' (Table 21). In harvests 2 and 3 a pattern developed in which the hybrids had a similar number of shoots as the parental mean, but the parents separated into two groups; the introduced populations (M81, M425, R,N) having higher shoot numbers and the remaining varieties (DP, HR, A,D) having lower numbers (Tables 22 and 23). The hybrids were intermediate between the two groups. There was no overall reciprocal effect for shoot number and only very few differences between male and female groups which may once again reflect the influence of extreme individual plants within one hybrid group.

There were some significant soil x population interactions for yield at harvest 1 and in the non-flooded treatment at harvest 2. In harvest 1 the interaction was caused by some low yield in the groundwater rendzina soil and in harvest 2 by approximately half of the populations not being significantly different between the solodized solonetz and lateritic podsol soils, but there was no consistent pattern in the performance of either parents or hybrid progeny, but the data is not presented because it does

TABLE 21.

The average number of shoots per plant of parents and hybrid progeny groups at Harvest 1.

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	1.52	1.87	1.72	1.80
M425	1.36	1.81	1.87	1.84
R	2.02	1.80	1.79	1.80
N	1.63	1.85	1.77	1.81
DP	1.40	1.67	1.89	1.78
HR	1.73	1.91	1.82	1.87
A	1.72	1.85	1.84	1.85
D	1.58	1.72	1.78	1.75

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.251	.330	.423
Means of 4 hybrids	.177	.233	.299
A Mean of 4 hybrids and any parent	.281	.369	.473
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	.266	.350	.449

TABLE 22.

The average number of shoots per plant of parents and hybrid progeny groups in the nonflooded control treatment at Harvest 2.

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	2.29	2.23	2.01	2.12
M425	2.86	2.59	2.27	2.43
R	3.17	2.10	2.25	2.18
N	2.04	2.22	2.29	2.26
DP	1.62	2.18	2.33	2.26
HR	1.91	2.17	2.34	2.26
A	1.88	2.27	2.29	2.28
D	2.12	2.19	2.19	2.19

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.383	.503	.645
Means of 4 hybrids	.271	.356	.456
A Mean of 4 hybrids and any parent	.428	.562	.721
Means of 8 hybrids	.192	.252	.323
A Mean of 8 hybrids and any parent	.406	.534	.684

TABLE 23.

The average number of shoots per plant of parents and hybrid progeny groups in the nonflooded control treatment at Harvest 3.

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	2.41	2.37	2.13	2.25
M425	3.03	2.87	2.45	2.65
R	3.06	2.26	2.19	2.23
N	2.39	2.37	2.25	2.31
DP	1.78	2.23	2.48	2.36
HR	1.85	2.31	2.53	2.42
A	1.80	2.19	2.57	2.38
D	1.82	2.26	2.29	2.28

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.386	.508	.651
Means of 4 hybrids	.273	.359	.460
A Mean of 4 hybrids and any parent	.432	.568	.728
Means of 8 hybrids	.193	.254	.326
A mean of 8 hybrids and any parent.	.409	.539	.691

not contain any consistent information to assist in understanding the relative waterlogging tolerance of the populations.

4.3.3.2. Growth of flooded populations

The overall effect of flooding on plant yield was severe, reducing the mean yield of parents by 83.4% and of hybrids by 84.9% (Table 24). Flooding caused marked differences in yields of the parents (Table 25) whereas in the non-flooded treatment the parents had similar yields (Table 19). Therefore in the flooded treatment plant yields demonstrate the difference in tolerance between the tolerant and intolerant parental groups. When flooded, parents ranged from the high yield of 'Marusinskaya 81' to the low yields of 'African' and 'Demnat', but all hybrid groups had similar yields intermediate between their parents. The hybrid vigour expressed in non-flooded conditions was lost.

At harvest 3 there were no significant differences in yield per plant between parents, parents and their progeny or between progeny group means. The overall mean yield per plant was 0.093 gm. The extreme variability in regrowth is reflected in the high values of least significant differences between populations which were 0.051gm at the 5%, 0.067gm at the 1% and 0.087gm at the 0.1% levels respectively. Some superior individual plants in the groundwater rendzina soil caused significant population differences but there was no consistent pattern (data not presented).

The pattern of shoot production after flooding was similar to the response of average plant yield. Although the mean reduction in shoot number was similar for parents and hybrids (Table 24) there were significant differences between parents (Table 26) reflecting their range of tolerance to flooding, but there was no significant differences between the progeny groups which again had a performance intermediate between parents. The differences between HR-male and HR-female, groups was caused by a few superior plants in the groundwater rendzina soil.

During regrowth the average number of shoots per regrowing plant

TABLE 24.

Percentage reduction in the yield and number of shoots per plant caused by flooding.

Population	Average dry weight per plant		Average number of shoots per plant	
	Parent	Hybrids	Parent	Hybrids
M81	72.5	84.3	38.8	51.9
M425	80.1	83.4	42.3	52.7
R	87.9	84.2	65.3	51.4
N	81.3	87.2	42.2	55.8
DP	86.7	84.4	50.0	53.1
HR	83.3	83.9	52.9	52.7
A	88.3	86.2	56.4	55.3
D	87.0	85.4	72.2	51.1
Means	83.4	84.9	52.5	53.0

TABLE 25.

The average dry weight per plant of parent and hybrid progeny groups in the flooded treatment at Harvest 2. (gm. per plant)

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	.079	.058	.040	.049
M425	.066	.063	.053	.058
R	.052	.052	.056	.054
N	.049	.053	.048	.051
DP	.042	.054	.055	.055
HR	.042	.046	.055	.051
A	.031	.047	.050	.049
D	.030	.048	.054	.051

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.024	.031	.040
Means of 4 hybrids	.017	.022	.028
A Mean of 4 hybrids and any parent	.026	.035	.045
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	.025	.033	.042

TABLE 26.

The average number of shoots per plant of parents and hybrid progeny groups in the flooded treatment at Harvest 2, adjusted for differences between soils at Harvest 1.

Population	Parent	Mean of Four Hybrids with common parent		Mean of all hybrid progeny
		Female	Male	
M81	1.40	1.13	0.91	1.02
M425	1.65	1.21	1.08	1.15
R	1.10	1.06	1.06	1.06
N	1.18	0.96	1.04	1.00
DP	0.81	1.08	1.04	1.06
HR	0.90	0.94	1.20	1.07
A	0.82	0.98	1.06	1.02
D	0.59	1.08	1.06	1.07

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.318	.419	.538
Means of 4 hybrids	.225	.296	.380
A Mean of 4 hybrids and any parent	.356	.468	.601
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	.337	.444	.571

differed significantly between parents but not between the means of hybrids (Table 27). 'Marusinskaya 425' had more shoots than its progeny and there was a tendency for the progeny of 'Du Puits', 'African' and 'Demnat' to be poor in shoot growth recovery.

Two factors present in the expression of shoot production under flooding are demonstrated by parental performance. Firstly the differences in shoot growth repression caused by flooding (Table 24) and secondly, the intrinsic differences between parents in shoot production demonstrated in the non-flooded treatment at harvest 3 (Table 23). This may be the major cause of differences in the flooded treatment at harvest 3 (Table 27), rather than the tolerance of varieties, because the ratio of regrowth of flooded and non-flooded treatments at harvest 3 were similar, being the following for each parent: M81, 0.61; M425, 0.60; R, 0.45; N, 0.56; DP, 0.62; HR, 0.71; A, 0.63; and D, 0.63.

There were no significant soil x population interactions for either yield or shoot production in the flooded treatment and the overall performance of populations was best in the groundwater rendzina soil and worst in the solodized solonetz.

In Fig. 10 the effect of flooding in the groundwater rendzina soil on 'Marusinskaya 81'($\frac{1}{2F}$) and 'Hunter River' ($\frac{6}{2F}$) and their reciprocal hybrids is illustrated. Note the difference in visual appearance of the parents and the intermediate performance of the hybrid populations.

4.3.4. The effect of flooding and soil type on the appearance of parental and hybrid populations

After flooding for 14 days the only differences between populations occurred in the solodized solonetz soil. The cultivars 'Hunter River', 'African' and 'Demnat' were severely affected at this stage whereas the four tolerant parents (M81, M425, R,N) were only slightly affected.

FIGURE 10.

The effect of flooding on the parents 'Marusinskaya 81' and 'Hunter River' and the reciprocal hybrids derived from them in the flooded groundwater rendzina soil at Harvest 2.

From left to right:

'Marusinskaya 81' $\overset{1}{(2F)}$; M81 x HR $\overset{10}{(2F)}$; HR x M81 $\overset{29}{(2F)}$;
and 'Hunter River' $\overset{6}{(2F)}$.

FIGURE 10.

TABLE 27.

The average number of shoots per regrowing plant of parents and hybrid progeny groups at Harvest 3 adjusted for differences between soils at Harvest 1.

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	1.46	1.28	1.20	1.24
M425	1.83	1.38	1.30	1.34
R	1.38	1.35	1.37	1.36
N	1.34	1.23	1.28	1.26
DP	1.11	1.30	1.33	1.32
HR	1.32	1.29	1.36	1.33
A	1.13	1.30	1.24	1.27
D	1.14	1.28	1.32	1.30

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.336	.443	.569
Means of 4 hybrids	N.S.	N.S.	N.S.
A Mean of 4 hybrids and any parent	.376	.495	.636
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	.356	.470	.604

There were no differences between hybrid groups which had mean scores between their respective parents (Table 28).

After 28 and 35 days of flooding the relationships between the scores of the parents and hybrids were similar. In Table 29 the scores after 28 days of flooding are presented. There were small differences between the mean scores of the hybrids which were generally more affected by flooding than the parental populations M81, M425, R and N, and less affected than the parental populations HR, A and D. Therefore the hybrids again had mean scores intermediate between the two different groups of parents. The high level of tolerance of the two Russian parents (M81 and M425) and some hybrid groups in the groundwater rendzina soil caused a significant soil x population interaction.

4.3.5. The effect of flooding on the meristemmatic activity of parental and hybrid populations

After flooding, the proportion of plants retaining meristemmatic activity ranged from 74% to 7%. Within the parents the introduced varieties (M81, M425, R,N) were generally significantly better than the other parents and their progeny groups, and 'Demnat' was worse than its progeny group (Table 30).

During regrowth many plants which had been seriously affected by flooding produced at least one shoot and therefore were classified as survivors. There were generally no differences between hybrid groups, however M81 was higher and 'Demnat' lower in regrowth performance than their respective progeny groups (Table 31).

There was not a significant soil x population interaction for the proportion of plants with meristemmatic activity after flooding or regrowth.

4.4. DISCUSSION AND CONCLUSIONS

The pattern of parental performance was the same as in Experiment 1

TABLE 28.

Scores of plant appearance of parents and hybrid progeny groups in the solodized solonetz soil after 14 days of flooding.

(1=control, 9=dead)

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	3.00	4.33	4.50	4.42
M425	2.67	4.34	5.08	4.71
R	2.00	3.83	4.59	4.21
N	2.33	4.09	3.92	4.01
DP	3.67	4.50	4.00	4.25
HR	5.00	5.00	3.75	4.38
A	5.33	4.00	4.50	4.25
D	6.00	4.58	4.33	4.46

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	1.79	2.38	3.08
Means of 4 hybrids	N.S.	N.S.	N.S.
A Mean of 4 hybrids and any parent	2.00	2.66	3.44
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	1.90	2.52	3.27

TABLE 29.

The plant appearance score of parental and hybrid group populations within and over all soils after 28 days of flooding (1=control, 9=dead)

Population	Soil						Average Score	
	Solodized Solonetz		Groundwater Rendzina		Lateritic Podsol			
	Par.	H.P.	Par.	H.P.	Par.	H.P.	Par.	H.P.
M81	6.00	7.25	2.00	4.92	5.00	5.29	4.33	5.82
M425	5.00	7.04	3.00	4.84	4.33	5.13	4.11	5.67
R	5.67	6.38	4.67	4.50	4.33	4.79	4.89	5.22
N	5.33	6.42	3.67	5.13	4.67	5.50	4.56	5.68
DP	6.33	7.00	4.67	4.71	5.67	4.75	5.56	5.49
HR	7.33	6.84	6.33	4.58	5.67	5.09	6.44	5.50
A	8.00	6.63	6.00	5.00	6.00	5.38	6.67	5.67
D	8.00	6.63	7.67	5.09	7.67	5.54	7.78	5.75

Table of L.S.D.'s.

Comparison between	.05	.01	.001
Overall parent average scores	.866	1.143	1.468
Overall means of 8 hybrids	.433	.572	.734
A mean of 8 hybrids & any parent	.918	1.212	1.557
Parents within the same soil	1.50	1.98	2.54
Soils at the same/different parent.	1.64	2.23	3.10
Hybrid means in the same soil	.75	.99	1.27
Soils at the same/different Hybrid group	.82	1.12	1.55

TABLE 30.

The proportion of plants present before flooding which were active at the apical meristem in parents and hybrid progeny groups at Harvest 2.

Population	Parent	Mean of Four Hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	.74	.35	.21	.28
M425	.66	.40	.34	.37
R	.41	.38	.37	.37
N	.52	.28	.27	.28
DP	.26	.33	.33	.33
HR	.28	.28	.46	.37
A	.28	.31	.32	.32
D	.07	.27	.30	.28

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.189	.249	.320
Means of 4 hybrids	.134	.176	.226
A Mean of 4 hybrids and any parent	.211	.278	.358
Means of 8 hybrids	N.S.	N.S.	N.S.
A Mean of 8 hybrids and any parent	.200	.264	.339

TABLE 31.

The proportion of plants present on the parents and hybrid progeny groups before flooding which developed new shoots during regrowth between Harvests 2 and 3.

Population	Parent	Mean of four hybrids with common parent as		Mean of all hybrid progeny
		Female	Male	
M81	.84	.67	.62	.64
M425	.85	.72	.69	.71
R	.86	.72	.71	.72
N	.87	.69	.72	.70
DP	.72	.68	.68	.68
HR	.75	.60	.73	.66
A	.73	.70	.67	.69
D	.48	.76	.73	.74

L.S.D.'s.

Comparison between	.05	.01	.001
Parents	.176	.292	.546
Means of 4 hybrids	N.S.	N.S.	N.S.
A Mean of 4 hybrids and any parent	.197	.326	.610
Means of 8 hybrids	.088	.146	.273
A Mean of 8 hybrids and any parent	.187	.310	.579

with a trend from high tolerance in the Russian varieties to very low tolerance in 'Demnat' and again the eight varieties tended to be in two groups of four, one group tolerant and the other more sensitive to flooding. The hybrids which had been developed by making all combinations between these two groups generally expressed an intermediate performance with little difference between the means of groups of hybrids derived from a common parent.

To assess the relative tolerance of populations, the measurement of the dry weight of herbage and the proportion of plants with meristemmatic activity were retained as variates, but in addition, in this experiment a score for plant appearance and a determination of the average number of shoots per plant were included. Plant appearance permits a progressive assessment of tolerance and shoot number assists in understanding the growth of the morphologically diverse populations.

As in Experiment 1 the highest yields and greatest retention of meristemmatic activity occurred in the groundwater rendzina soil. The least effect of flooding when determined by visual assessment also occurred in the groundwater rendzina and the greatest effect was with the solodized solonetz. The number of shoots was also greatest in the groundwater rendzina soil in the non-flooded treatment and in the same soil during regrowth after flooding. During flooding there were no differences in shoot production between soils indicating that flooding was the dominant factor in affecting the shoot production of lucerne in the three soils studied.

There was a consistent relationship between the four criteria of assessment yield, shoot number, plant appearance and meristemmatic activity. Plants of the most tolerant populations (the four tolerant parents) and plants growing in the least affected soil treatment (Groundwater rendzina) were higher yielding, retained a higher proportion of meristemmatic activity and were visually assessed as being less damaged. The tolerant populations have a higher propensity to produce shoots under non-flooded conditions but their higher shoot production after flooding may be a reflection of this characteristic rather than a differential effect of flooding.

There were no significant soil x population interactions in the flooded treatment except that caused by the high tolerance of the Russian varieties in the groundwater rendzina in the visual assessment. Therefore the pattern of performance of the parents and hybrids when flooded and during regrowth after flooding was similar in each soil.

The heterotic effect expressed by yield in the non-flooded treatment was apparently caused by the larger size of individual shoots in hybrids, but flooding reduced the growth rate of individual shoots and the heterotic effect was lost.

In crossing heterozygous parent plants, the hybrid populations express a wide range of combinations and the variation from plant to plant in hybrid populations appeared greater than in the parental populations. Therefore at the end of the flooding period it was noted that some hybrid plants which had retained meristemmatic activity were much larger individually than those in the tolerant varieties although the mean performance of the hybrid populations was less than the mean plant performance in tolerant varieties. Also during regrowth the high variation in the data was caused by a number of individual plants which had higher shoot numbers and regrowth vigour.

5. EXPERIMENT 3: THE RESPONSE OF SELECTED PARENTAL AND HYBRID CLONES TO WATERLOGGING UNDER FIELD CONDITIONS

5.1. INTRODUCTION

The parental and hybrid populations grew actively under the temperature and light regimes imposed in the two previous experiments although a range of winter growth rates would be expected in the winter under field conditions in southern Australia. The variation in winter growth rate would be expected to range from the extreme winter dormancy of the Russian and North American parents and the moderately high winter dormancy of the Flemish variety 'Du Puits' to the slow winter growth of 'Hunter River' and the extreme winter activity of the varieties of North African origin, 'African' and 'Demnat' (Rogers and Bailey, 1968; Leach 1971).

Varieties which are more winter dormant than 'Hunter River' usually are also lower yielding in the late autumn or early spring and are less acceptable as pasture varieties. Therefore the selection of waterlogging tolerance must be done in conjunction with selection for a winter yielding ability equal or superior to that of 'Hunter River'.

In this experiment selected clones from Experiment 2 were grown in the field. A harvest taken at the beginning of winter measured the yield potential of the clones under non-waterlogged conditions and in a subsequent harvest, taken after flooding the experiment, the survival and growth during flooded conditions were measured. An assessment of the effectiveness of selection for waterlogging tolerance based on regrowth of plants which survived flooding in the glasshouse was made from comparisons of selected and randomly chosen populations.

5.2. EXPERIMENTAL METHODS

5.2.1. Selection and establishment of clonal material

Twelve populations of the forty studied in Experiment 2 were chosen for further investigation in the experiment. They were:

Marusinskaya 81 (M81)
Narragansett (N)
Hunter River (HR)
Demnat (D)
M81 x HR and the reciprocal cross HR x M81
M81 x D and the reciprocal cross D x M81
N x HR and the reciprocal cross HR x N
N x D and the reciprocal cross D x N

These populations were chosen because they encompass the range of tolerance found in the eight parents in Experiments 1 and 2 and include a representative variety from the U.S.S.R. and from North America, the predominant Australian variety 'Hunter River' and the variety 'Demnat' of Moroccan origin which has been registered in Australia because of its winter growth. The hybrids represent reciprocals of an orthogonal topcross between the tolerant (M81, N) and intolerant (HR, D) varieties.

Two groups of plants were selected from within each population.

Group 1: Five plants which expressed the best regrowth after surviving the flooding treatment in the solodized solonetz soil in Experiment 2 were taken from each of the parental and hybrid populations. The plants were selected from all of the three replicates.

Group 2: Ten plants from each population chosen randomly from the non-flooded treatment in Experiment 2 as a nonselected control.

The five selected clones were chosen from a total of thirty plants per population representing a selection of one in six. Ten control clones were taken from each population to reduce the random sampling error which may result from a sample of only five clones and yet allow statistical analysis of the means of the selected and control groups.

The inclusion of more than ten clones would have made the experiment considerably larger and it was considered that more than ten clones would not have greatly improved the estimate of the means of the control populations.

The selected clones were transplanted after harvest 3 in Experiment 2. Cuttings from each of the 180 clones were struck in a moistened mixture of perlite and sandy loam during December 1974 and transplanted in February 1975 into waxed paper cups (10 cm x 6 cm) containing a sandy loam potting soil. The clones were trimmed back to within 5 cm of the crown and planted in the field on March 5 and 6, 1975. The paper cups were removed before planting. Superphosphate was applied at 200 k ha^{-1}. After establishment the plants were cut back to 5 cm above the crown and plot area was sprayed with 'Gramoxone' at the rate of 1.5 l. ha^{-1} to control weeds on April 28, 1975.

5.2.2. Experimental design and measurements

The twelve populations of clones were planted in a randomized block design having four replications. Within each of the twelve population blocks the fifteen clones (5 selected and 10 control) were randomly positioned in a 5 x 3 arrangement in a square grid with 30 cms between plants. The overall experiment was a 30 plant x 24 plant grid of plants at 30 cm x 30 cm spacing with randomly chosen plants from surplus cuttings as a single border row.

After cutting back on April 28 the plants were allowed to regrow until June 3 when Harvest 1 was taken. At this harvest the following measurements and scores were taken:

(1) The height of the undisturbed plant

(2) The length of the longest stem arising from the crown

(3) The number of shoots greater than 5 cm long arising from the crown

(4) The dry matter yield of shoots

An index of plant morphology was calculated by deriving the ratio of measurements (1) and (2). This is a measure of shoot inclination and the erectness of plant growth and is conceptually related to the trigonometrical ratio, sine.

On July 22, harvest 2 was taken and the same measurements made. On six occasions, that is once weekly between Harvest 1 and Harvest 2, a score of plant appearance was obtained based on the scale used in Experiment 2. On September 2 the number of surviving clones was noted.

5.2.3. Experimental site and management of the soil moisture regime

The site was on the western boundary of Section 339, Hundred of Kuitpo, South Australia. This site is prone to winter waterlogging and is a duplex soil of sand with clay at depth and is within the Meadows Fine Sand Soil association (Rix and Hutton, 1953). A description of the soil profile is given in Appendix 7.

Before the plants were established on the site, a sprinkler irrigation of 15 cms was applied and thereafter the site was irrigated by hand watering at a rate sufficient to compensate for evaporation. The site is part of an irrigated farm.

This form of irrigation was continued until Harvest 1 (June 3, 1975). Thereafter the site was flooded with two to three centimetres of water per day and allowed to drain so that after two or three hours no part was immersed deeper than approximately one centimetre. The watertable rose in the experimental site and the water content of the soil profile rose above that present at Harvest 1 (Tables 32 and 33). After twenty eight days of irrigation the site was waterlogged except for a shallow surface horizon which was saturated to field capacity.

The experiment was conducted during late autumn and winter to permit maximum differentiation of the winter growth patterns and survival in a winter environment of the plant material. The average weekly minimum, maximum and mean air temperatures at the nearest meteorological station

TABLE 32.

Soil Moisture Content (gm. water per 100 gm. dry soil) in six profile sections.

Section of the profile (depth, cms.)	Date (weeks of flooding)				
	3/6/75 (0)	1/7/75 (4)	8/7/75 (5)	15/7/75 (6)	22/7/75 (7)
0-10	17.5	51.5	45.1	50.0	45.7
10-20	15.4	24.3	24.9	24.6	24.1
20-30	15.8	19.8	16.9	17.8	16.5
30-40	17.1	18.3	19.0	19.1	17.2
40-50	22.0	25.0	29.5	26.8	30.8
50-60	27.8	32.5	38.4	36.6	37.6

TABLE 33.

Depth to the Free Water Table during Flooding.

Date	Days of Flooding	Depth (cms.)
3-6-75	0	60
10-6-75	7	25
17-6-75	14	18
24-6-75	21	15
1-7-75	28	11
8-7-75	35	3
15-7-75	42	1
22-7-75	49	<1

(Mount Barker) are presented in Appendix 8 for every week in the growth periods prior to Harvests 1 and 2.

5.3. RESULTS AND DISCUSSION

5.3.1. Overall comparison of the selected and control clones

The overall comparison of the selected and randomly chosen control clones indicated that significant differences of plant measurements and scores only occurred for the number of shoots per plant at each harvest and the appearance of plants after thirty five days of flooding (Table 34).

When the selected clones were chosen during the regrowth period in Experiment 2 no emphasis was placed upon the appearance which the clones had during the previous flooding treatment, but the scores of the selected group were consistently lower although significant only on day 35 (Table 34). This difference indicates that the appearance of the selected clones was less affected by flooding.

5.3.2. Comparisons between selected and control clones within populations

Significant population x selection group interactions occurred for eight plant measurements and were caused by differences between the selected and randomly chosen clones for one or more measurements in seven of the twelve populations. Only the populations which caused the significant interactions and the plant measurements in which they occurred are listed in Table 35.

These significant interactions were associated with the superior performance of a number of clones within the selection group in which the larger measurement occurred in the comparison between groups (Table 35). These clones generally had values differing significantly from all other clones, whether in the selected or random groups, within each population (data not presented). The number of such superior clones in each population and the selection group in which they occurred were:

TABLE 34.

Overall comparison of the control and selected groups.

Plant Measurement or Score	Group		L.S.D.'s.
	Control	Selected	.05; .01; .001
Harvest 1			
Plant Height (cm.)	14.53	14.44	N.S.
Shoot Length (cm.)	21.60	21.12	N.S.
No. of Shoots	8.21	8.81	0.60; 0.78; 1.00
Dry Weight (gm)	1.93	2.06	N.S.
Av. Dry Wt. per Shoot	0.23	0.22	N.S.
Inclination (sine)	0.62	0.64	N.S.
Harvest 2			
Plant Height (cm.)	4.90	5.51	N.S.
Shoot Length (cm.)	7.16	7.75	N.S.
No. of Shoots	4.22	4.89	0.53; 0.70; 0.89
Dry Weight (gm.)	0.53	0.62	N.S.
Av. Dry Wt. per Shoot	0.11	0.11	N.S.
Inclination (sine)	0.65	0.67	N.S.
Visual Scores *			
14 Days of Flooding	1.45	1.45	N.S.
21 Days of Flooding	2.29	2.16	N.S.
28 Days of Flooding	2.58	2.46	N.S.
35 Days of Flooding	3.72	3.42	0.26; 0.34; 0.44
42 Days of Flooding	4.51	4.24	N.S.
49 Days of Flooding	5.47	5.25	N.S.

* The visual scores were on a scale from 1 (unaffected by flooding) to 9 (apparently dead with no leaf tissue remaining).

TABLE 35.

Comparisons of plant measurements within populations for which significant differences occurred between the control and selected groups of clones.

Plant Measurement	Population or Hybrid	Selection Group		L.S.D.'s.
		Control	Selected	.05; .01; .001
Height (Harvest 1)	HR × N	12.37	15.22	2.78; 3.64; 4.66
	D × M81	18.35	21.65	
Shoot Length (Harvest 1)	N × D	29.28	24.60	3.43; 4.49; 5.74
	HR × N	20.09	23.85	
	D × M81	24.96	29.40	
Dry Weight (Harvest 1)	Demnat	3.00	3.72	0.69; 0.91; 1.16
	HR × N	1.67	2.47	
	D × M81	2.53	3.61	
Av. Dry Wt. (Harvest 1)	D × M81	0.26	0.33	0.06; 0.08; 0.10
Plant Inclination (Sine, Harvest 1)	M81 × HR	.379	.532	.075; .098; .125
	N × HR	.614	.518	
Height (Harvest 2)	Demnat	11.72	16.32	2.24; 2.93; 3.75
Shoot Length (Harvest 2)	Demnat	12.61	18.21	2.66; 3.49; 4.46
No. of shoots per plant (Harvest 2)	M81	2.02	4.10	1.84; 2.41; 3.08
	Demnat	4.67	8.21	
	N × D	6.60	4.50	

Population	No. of Clones	Selection Group
HR x N	3	Selected
D x M81	3	Selected
N x D	3	Control
Demnat	3	Selected
N x HR	3	Control
M81 x HR	2	Selected
Marusinskaya 81	4	Selected

The pattern of significant differences which occurred at Harvest 1 (taken before flooding) was not repeated at Harvest 2 (taken after flooding). The hybrids (HR x N) and (D x M81) contributed seven of the eleven differences occurring at Harvest 1 and another two populations, (M81 x HR) and (N x HR) expressed differences in morphology but none of these differences were repeated after flooding at Harvest 2. The superior clones of the populations (N x D) and 'Demnat' caused significant differences in different plant measurements at each harvest. (N x D) was the only population in which the superior clones contributing to plant growth occurred in the non-selected control group. The superior 'Demnat' clones only expressed higher dry weight at Harvest 1, but this advantage was lost under flooded conditions and superiority was expressed in plant height, shoot length and shoot number.

Although the shoot number per plant was the only overall significant difference in plant growth at the individual population level, higher values in the selected group were only expressed by the parents 'Marusinskaya 81' and 'Demnat' at Harvest 2. The controls were superior in (N x D) in opposition to the general trend because of the superior performance of three control clones.

No population caused a significant population x selection group interaction in scores for plant appearance.

In Figure 11 is illustrated one replicate of the 'Demnat' population demonstrating the height, shoot length and shoot production of the superior clones.

5.3.3. Comparison of parental and hybrid populations

Because there were few significant differences between the selected and control groups of any one population the groups were combined and comparisons made between the populations. The analysis permitted the following comparisons.

1. Individual parents with hybrids (Tables 36, 38 and 40)
2. Between the means of groups of four hybrids with a common parent (Tables 37, 39 and 41)
3. Between the means of groups of four hybrids and any parent (Tables 37, 39 and 41)
4. Between reciprocal crosses (Tables 36, 38 and 40)

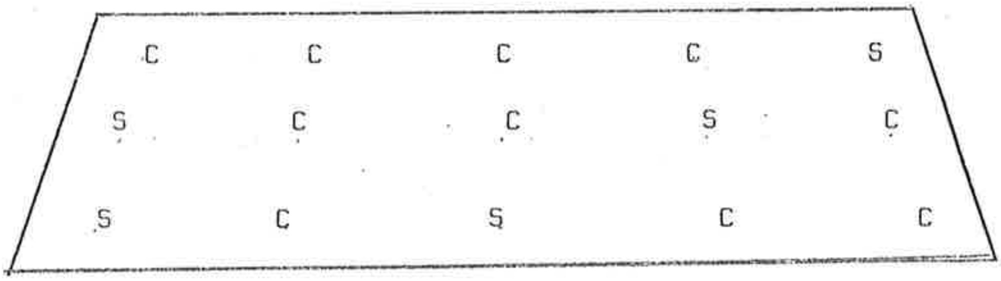
Under non-flooded field conditions in late autumn the four parental populations had different growth rates. This is reflected in the length and number of shoots and the dry matter per plant and per shoot (Table 36). 'Marusinskaya 81' had the lowest growth rate, 'Narragansett' and 'Hunter River' were intermediate and 'Demnat' was the most active. The ratio of shoot height to length (sine) demonstrates the difference in morphology between the parents. 'Marusinskaya 81' and 'Narragansett' are semi-prostrate and 'Hunter River' and 'Demnat' erect.

In both harvests, individual hybrids and the means of reciprocal hybrid pairs had values generally between their two parents or not significantly different from one or other parent. The parental combinations in which the reciprocals had significantly different values are indicated by an asterisk in Tables 36, 38 and 40.

FIGURE 11.

The variety 'Demnat' after seven weeks of flooding in the field.

The clone in the top right-hand corner of the delineated sub-block was the most tolerant and highest yielding clone in the plot of individual plant performance in Figure 12.



C - control clones

S - selected clones

FIGURE 11.

TABLE 36.

Plant growth measurements of each parental and hybrid population at Harvest 1.

Population	Plant Measurement					
	Height	Length	Shoot No.	Dry Wt.	Av. D.Wt.	Sine
Marusinskaya 81	3.09	9.15	4.33	0.81	0.16	.337
Narragansett	8.15	17.09	7.90	1.38	0.17	.479
Hunter River	15.97	21.52	8.04	1.54	0.19	.746
Demnat	30.31	35.57	8.03	3.27	0.40	.860
M81 x HR	6.68*	15.03*	9.20*	1.43	0.14	.430*
HR x M81	9.14*	17.49*	5.66*	0.96	0.16	.517*
M81 x D	13.86*	20.70*	9.33	2.43	0.24*	.650*
D x M81	19.16*	25.93*	10.55	2.85	0.29*	.733*
N x HR	10.53*	18.00*	8.34	1.51	0.18	.584*
HR x N	13.04*	20.95*	9.07	1.90	0.20	.643*
N x D	21.82	27.67	10.23	2.75	0.27	.779
D x N	21.68	26.86	9.45	2.76	0.28	.800
Means	14.45	21.33	8.34	1.97	0.22	.630
L.S.D.'s. between populations.						
.05	1.70	2.12	1.66	0.52	0.04	.051
.01	2.28	2.79	2.22	0.69	0.06	.068
.001	3.02	3.69	2.94	0.92	0.07	.090

TABLE 37.

Plant growth measurements of parents and hybrid progenies after grouping at Harvest 1. **

Population or Group of hybrids	Plant Measurement					
	Height	Length	Shoot No.	Dry Wt.	Av.D.Wt.	Sine
Marusinskaya 81	3.09	9.15	4.33	0.81	0.16	.337
Narragansett	8.15	17.09	7.90	1.38	0.17	.479
Hunter River	15.97	21.52	8.04	1.54	0.19	.746
Demnat	30.31	35.57	8.03	3.27	0.40	.860
M81/HR Hybrids	7.91	16.26	7.43	1.20	0.15	.474
M81/D Hybrids	16.51	23.32	9.94	2.64	0.27	.692
N/HR Hybrids	11.79	19.48	8.71	1.71	0.19	.614
N/D Hybrids	21.75	27.27	9.84	2.76	0.20	.790
M81 Hybrids	12.21	19.79	8.69	1.92	0.21	.583
N Hybrids	16.77	23.38	9.28	2.24	0.24	.702
HR Hybrids	9.85	17.87	8.07	1.46	0.17	.544
D Hybrids	19.13	25.30	9.89	2.70	0.28	.741

L.S.D.'s. Between

Any parent & the mean of reciprocals	.05	2.08	2.60	2.03	0.64	0.05	.062
	.01	2.79	3.42	2.72	0.84	0.07	.083
	.001	3.70	4.52	3.60	1.13	0.09	.110
Any parent & the mean of 4 hybrids	.05	1.90	2.37	1.86	0.58	0.04	.057
	.01	2.55	3.12	2.48	0.77	0.07	.076
	.001	3.37	4.13	3.29	1.03	0.08	.101
The means of reciprocals	.05	1.70	2.12	1.66	0.52	0.04	.051
	.01	2.28	2.79	2.22	0.69	0.06	.068
	.001	3.02	3.69	2.94	0.92	0.07	.091
The means of any two groups of 4 hybrids	.05	1.20	1.50	1.17	0.37	0.03	.036
	.01	1.61	1.97	1.57	0.49	0.04	.048
	.001	2.14	2.61	2.08	0.65	0.05	.064

** The parental measurements are identical to those presented in Table 36 and are presented here for comparison with the hybrid groups.

TABLE 38.

Plant growth measurements of each parental and hybrid population at Harvest 2.

Population	Plant Measurement					
	Height	Length	Shoot No.	Dry Wt.	Av.D.Wt.	Sine
Marusinskaya 81	1.62	3.12	2.71	0.15	0.06	.551
Narragansett	3.00	4.92	3.07	0.23	0.07	.604
Hunter River	3.97	5.33	2.72	0.30	0.10	.716
Demnat	13.25	14.48	5.85	1.32	0.22	.905
M81 x HR	2.68	4.85	3.90	0.32	0.08	.546
HR x M81	3.19	5.83	2.91	0.28	0.09	.532
M81 x D	5.65	8.52	5.22	0.67	0.12	.669
D x M81	6.74	9.54	6.21	0.89	0.14	.695
N x HR	4.40	7.24	4.76	0.45	0.09	.627*
HR x N	4.13	7.70	5.96	0.67	0.11	.535*
N x D	7.10	9.44	5.90	0.85	0.14	.735
D x N	5.52	7.35	4.10	0.59	0.12	.759
Means	5.10	7.36	4.41	0.56	0.11	0.656
L.S.D.'s. between populations.						
.05	3.01	3.03	2.11	0.36	0.03	.072
.01	3.85	4.07	2.96	0.48	0.04	.097
.001	5.09	5.38	3.75	0.64	0.06	.129

TABLE 39.

Plant growth measurements of parents and hybrid progenies after grouping at Harvest 2. **

Population or Group of hybrids	Plant Measurement					
	Height	Length	Shoot No.	Dry Wt.	Av.D.Wt.	Sine
Marusinskaya 81	1.62	3.12	2.71	0.15	0.06	.551
Narragansett	3.00	4.92	3.07	0.23	0.07	.604
Hunter River	3.97	5.33	2.72	0.30	0.10	.716
Demnat	13.25	14.48	5.85	1.32	0.22	.905
M81/HR Hybrids	2.94	5.34	3.41	0.30	0.09	.539
M81/D Hybrids	6.20	9.03	5.72	0.78	0.13	.682
N/HR Hybrids	4.27	7.47	5.36	0.56	0.10	.581
N/D Hybrids	6.31	8.40	5.00	0.72	0.13	.747
M81 Hybrids	4.57	7.19	4.57	0.54	0.11	.611
N Hybrids	5.29	7.94	5.18	0.64	0.12	.664
HR Hybrids	3.61	6.41	4.39	0.43	0.10	.560
D Hybrids	6.26	8.72	5.36	0.75	0.13	.715

L.S.D.'s. between							
Any parent & the mean of reciprocals	.05	3.69	3.71	2.58	0.44	0.04	.088
	.01	4.72	4.99	3.63	0.59	0.05	.119
	.001	6.24	6.59	4.59	0.78	0.07	.144
Any parent & the mean of 4 hybrids	.05	3.37	3.39	2.36	0.40	0.03	.081
	.01	4.30	4.55	3.31	0.54	0.04	.108
	.001	5.69	6.01	4.19	0.72	0.07	.144
The means of reciprocals	.05	3.01	3.03	2.11	0.36	0.03	.072
	.01	3.85	4.07	2.96	0.48	0.04	.097
	.001	5.09	5.38	3.75	0.64	0.06	.129
The means of any two groups of 4 hybrids	.05	2.13	2.14	1.49	0.24	0.02	.051
	.01	2.72	2.88	2.09	0.34	0.03	.069
	.001	3.60	3.80	2.65	0.45	0.04	.091

** The parental measurements are identical to those presented in Table 38 and are presented here for comparison with the hybrid groups.

TABLE 40.

Scores for plant appearance of the parental and hybrid populations at six times after the commencement of flooding. (1 = unaffected, 9 = dead)

Population	No. of days of flooding					
	14	21	28	35	42	49
Marusinskaya 81	1.01	1.78	2.19	3.53	4.65	5.11
Narragansett	1.05	1.71	1.71	3.06	4.19	5.19
Hunter River	1.72	3.08	4.15	5.34	6.31	7.46
Demnat	2.37	3.48	3.58	4.54	5.44	6.05
M81 x HR	1.17	2.02	2.17	3.65	4.48	5.58
HR x M81	1.33	2.00	2.30	3.54	4.31	5.43
M81 x D	1.43	1.90*	2.02	2.89	3.38	4.51
D x M81	1.54	2.44*	2.40	2.99	3.74	4.67
N x HR	1.29	1.87	2.02	2.67	3.30	4.40
HR x N	1.16	1.87	2.12	3.14	3.66	4.63
N x D	1.56	2.28	2.83	3.96	4.28	5.22
D x N	1.78	2.56	3.05	4.15	5.25	6.47
Means	1.45	2.25	2.54	3.62	4.42	5.40
L.S.D.'s. between populations.						
.05	0.35	0.49	0.91	1.20	1.37	1.58
.01	0.47	0.65	1.23	1.61	1.84	2.12
.001	0.62	0.87	1.62	2.13	2.44	2.80

TABLE 41.

Scores for plant appearance at six times after the commencement of flooding for the parents and hybrid progenies after grouping.

(1 = unaffected, 9 = dead) **

Population or Group of hybrids	No. of days of flooding 14	21	28	35	42	49
Marusinskaya 81	1.01	1.78	2.19	3.53	4.65	5.11
Narragansett	1.05	1.71	1.71	3.06	4.19	5.19
Hunter River	1.72	3.08	4.15	5.34	6.31	7.46
Demnat	2.37	3.48	3.58	4.54	5.44	6.05
M81/HR Hybrids	1.25	2.01	2.24	3.60	4.40	5.50
M81/D Hybrids	1.49	2.17	2.21	2.94	3.56	4.59
N/HR Hybrids	1.23	1.87	2.07	2.91	3.48	4.52
N/D Hybrids	1.67	2.42	2.94	4.06	4.77	5.85
M81 Hybrids	1.37	2.09	2.23	3.27	3.98	5.05
N Hybrids	1.45	2.15	2.51	3.49	4.12	5.19
HR Hybrids	1.24	1.94	2.16	3.26	3.94	5.01
D Hybrids	1.58	2.30	2.58	3.50	4.17	5.22

L.S.D.'s Between		14	21	28	35	42	49
Any parent & the mean of reciprocals	.05	0.43	0.60	1.11	1.47	1.68	1.94
	.01	0.58	0.80	1.51	1.97	2.25	2.60
	.001	0.76	1.07	1.98	2.61	2.99	3.43
Any parent & the mean of 4 hybrids	.05	0.39	0.55	1.02	1.34	1.53	1.77
	.01	0.53	0.73	1.38	1.80	2.06	2.37
	.001	0.69	0.97	1.81	2.38	2.73	3.13
The means of reciprocals	.05	0.35	0.49	0.91	1.20	1.37	1.58
	.01	0.47	0.65	1.23	1.61	1.84	2.12
	.001	0.62	0.87	1.62	2.13	2.44	2.80
The means of any two groups of 4 hybrids	.05	0.25	0.35	0.64	0.85	0.97	1.12
	.01	0.33	0.46	0.87	1.14	1.30	1.50
	.001	0.44	0.62	1.15	1.51	1.72	1.98

** The parental measurements are identical to those presented in Table 40 and are presented here for comparison with the hybrid groups.

These differences were most common in Harvest 1 and were not repeated in Harvest 2, and could have been the result of superior growth of a small number of clones in the crosses HR x M81, HR x N and D x M81 which were tall, more erect and had longer shoots than other clones within these populations or their reciprocals. Hybrid vigour was not common and was only significantly expressed for the number of shoots per plant in (D x M81) and (N x D) in Harvest 1 and (HR x N) in Harvest 2 and for plant yield in (HR x N) in Harvest 2.

The mean performance at Harvest 1 of groups of four hybrids having a common parent generally demonstrates the intermediate values of plant measurements between the winter dormant varieties 'Marusinskaya 81' and 'Narragansett' and the more active varieties 'Hunter River' and 'Demnat'. Shoot number was the only plant character which did not have this pattern; the hybrids being equivalent to the more productive parents, 'Hunter River' and 'Demnat'. Among the hybrids measurements were generally lowest for the 'Hunter River' group, reflecting the lack of 'Demnat' parentage in this group (Table 37).

In Harvest 2 the mean of plant measurements of the pairs of reciprocals or groups of hybrids with a common parent was generally not significantly different from the performance of their respective parents or common parent except for the lower yields of 'Marusinskaya 81' and 'Narragansett' and the generally superior performance of 'Demnat' (Table 39).

The mean plant appearance of groups of four hybrids was generally similar but comparisons of the means with the common parents showed that the hybrids were not generally more affected than the two more tolerant parents and were significantly less affected by flooding than the intolerant varieties 'Hunter River' and 'Demnat' (Table 41).

In Harvest 2 the pattern of growth of the parental populations was similar to that at Harvest 1 (Table 38) but the visual appraisal of plant tolerance at intervals of seven days (Table 40) showed differences in sensitivity to flooding before the watertable approached the soil surface. At 14 days 'Demnat' was most affected, 'Hunter River' was intermediate and 'Marusinskaya 81' and 'Narragansett' were virtually unaffected. The division of the parents into tolerant (M81, N) and intolerant (HR, D) varieties was evident on days 21 and 28, and subsequent assessments for a completely waterlogged soil profile (Table 33) showed the extreme sensitivity of 'Hunter River' and 'Demnat' and a decline in the appearance of 'Marusinskaya 81' and 'Narragansett'. The regrowth of clones in the two or three weeks immediately following Harvest 1 contributed most to the plant measurements and yields taken at Harvest 2. The onset of waterlogging severely restricted growth in all but a few clones in the experiment.

5.3.4. Selection of individual clones which are tolerant to flooding and agronomically suitable for southern Australia

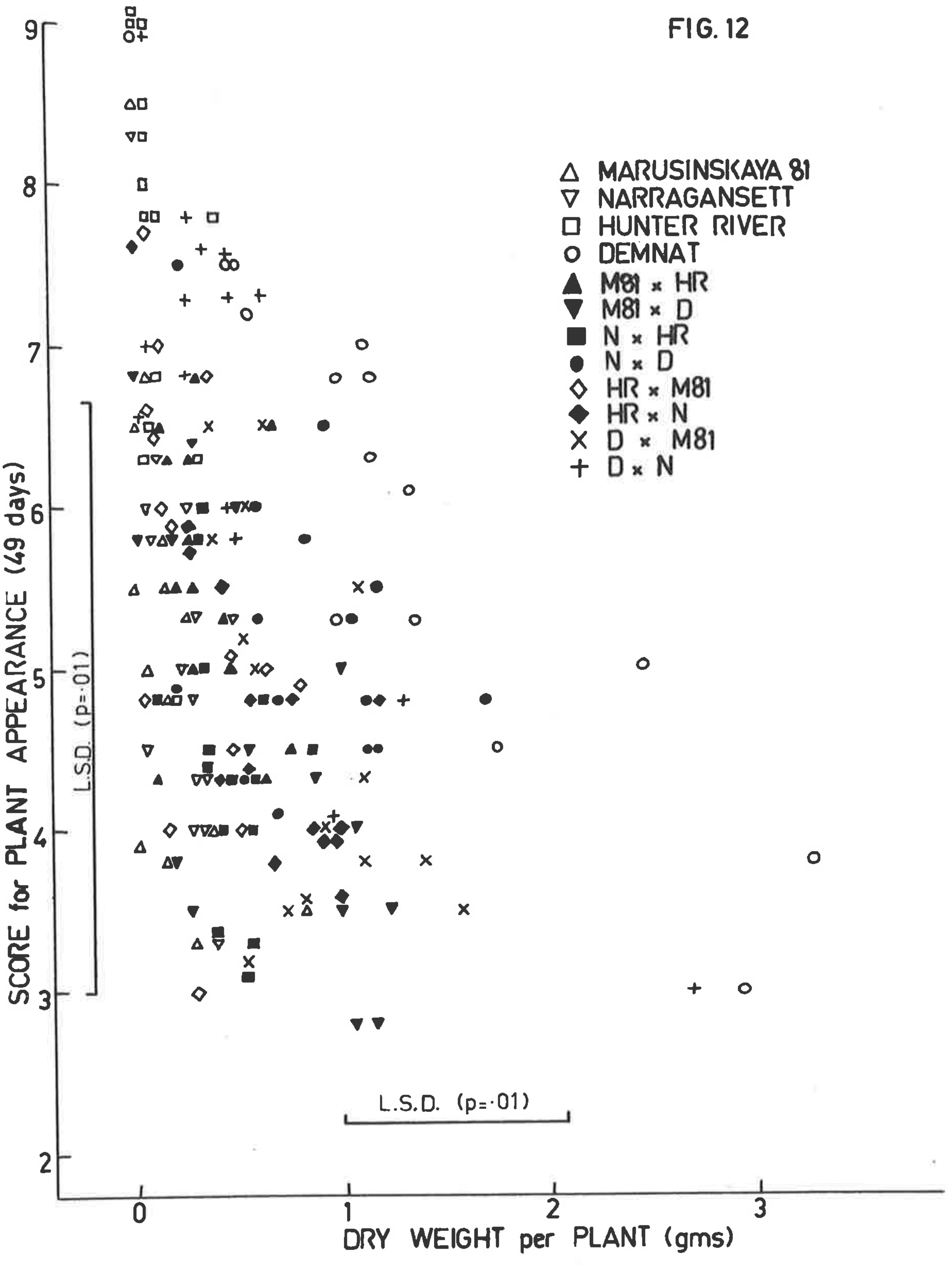
The design of this experiment permitted not only a comparison of parental and hybrid populations, but also the 180 individual clones representing those populations.

A comparison of clones is presented in Figure 12 using the visual score at day 49 as an index of tolerance (y axis) and the yield per clone at Harvest 2 as a measure of yield potential under flooded conditions (x axis). The plot demonstrates the range of tolerance and yielding ability of the material under flooded conditions. There was a wide range of tolerance in the introduced parents 'Marusinskaya 81' and 'Narragansett' but no significant differences between the yields of the clones. The clones of 'Hunter River' were extremely intolerant and this was reflected in low yields although under non-flooded conditions their average yield was moderately high (Table 36). The extreme range of variability in the 'Demnat' population was unexpected following the poor performance of the variety in the glasshouse experiments. 'Demnat' clones encompassed the range from the most sensitive to flooding to the most tolerant and highest yielding.

FIGURE 12.

The score for plant appearance (1 = unaffected; 9 = dead) and dry weight (gm per plant) of each clone of the four parents and eight hybrid populations after seven weeks of regrowth under flooded conditions.

FIG. 12



△ MARUSINSKAYA 81
▽ NARRAGANSETT
□ HUNTER RIVER
○ DEMNAT
▲ M81 × HR
▼ M81 × D
■ N × HR
● N × D
◇ HR × M81
◆ HR × N
× D × M81
+ D × N
SCORE for PLANT APPEARANCE (49 days)
L.S.D. (p=·01)
9
8
7
6
5
4
3
2
L.S.D. (p=·01)
0
1
2
3
DRY WEIGHT per PLANT (gms)

Many hybrid clones were both tolerant to flooding and had moderate to high yields. One clone of (D x N) gave an extreme expression of the combination of high yield and tolerance sought in making the crosses between Australian and introduced varieties. Therefore many hybrid clones did not express the winter dormancy of the introduced parents 'Marusinskaya 81' and 'Narragansett' or the extreme sensitivity to flooding of the dominant Australian variety 'Hunter River'. Also, a larger proportion of hybrids than of the 'Demnat' clones expressed tolerance.

The plot in Figure 12 shows that no clones were unaffected by flooding for 49 days although the better clones were only lighter in appearance than healthy clones (Score 3). No clones which were severely affected by flooding using the visual index expressed high yields under flooding.

After thirteen weeks of flooding all the surviving clones were hybrids except for four clones of the parent 'Narragansett' (Table 42). Clones which contributed surviving plants were present in all hybrid populations and occurred with approximately equal frequency in the hybrids derived from each parent (Marusinskaya 81, 48.4%; Narragansett, 46.8%; Hunter River, 41.6%; and Demnat, 53.2%). A statistical analysis of the yields of the surviving clones was not possible because the surviving clones were only present in one or two replicates and represented 12.7% of the original plant population. Some clones of the winter-dormant parents, 'Marusinskaya 81' and 'Narragansett' may have been extremely dormant having no top growth and were therefore undetected, but most appeared to have died after submergence in the surface water retained on the site after flooding and rainfall. The four surviving 'Narragansett' clones were not completely winter-dormant. The crowns of the 'Hunter River' and 'Demnat' clones had rotted and their top growth had collapsed and decayed. The surviving clones had retained meristemmatic activity and green leaf tissue although some had a high proportion of senescence. Tolerant clones occurred with approximately equal frequency in the control (32.5%) and selected (36.7%) groups.

TABLE 42.

The number of clones in each population having at least one surviving plant after thirteen weeks of flooding.

(* The number of clones which survived in two replicates)

Population	No. of clones surviving in at least one replicate		
	Selection Group		
	Control	Selected	Total
M81	0	0	0
N	4 (1)*	0	4
HR	0	0	0
D	0	0	0
M81 x HR	4 (1)	1	5
HR x M81	3	2 (1)	5
M81 x D	4 (2)	4 (2)	8
D x M81	7	4	11
N x HR	4	4 (1)	8
HR x N	4 (3)	3	7
N x D	6 (2)	0	6
D x N	3	4	7
Total	39	22	61
Hybrids derived from:			
M81	18	11	29
N	17	11	28
HR	15	10	25
D	20	12	32

All other hybrid clones in the experiment were severely rotted, had no active leaf tissue and many had disappeared.

5.4. SUMMARY

Under non-flooded field conditions in late autumm the four parental populations were significantly different in yield, expressing different levels of winter growth activity. The mean performance of hybrid populations was generally intermediate between parents.

After flooding was commenced the growth of each clone was determined by the interrelation of three factors; its winter growth, its adaptation to the rising watertable and saturated soil surface which were present for four weeks after Harvest 1 and its survival in the subsequent period of completely waterlogged conditions. After Harvest 1 the growth of the populations was similar to that under nonflooded conditions but the visual assessment of plants shows that at the population level the introduced parents and the hybrids were more tolerant than the Australian varieties. At the clonal individual plant level the variation of tolerance within populations was high, particularly in the parent 'Demnat'. At Harvest 2 clones which were only slightly affected by flooding were present in the parents 'Marusinskaya 81', 'Narragansett' and 'Demnat', and in many hybrid populations, but there was a wide range in the yield of these clones under flooded conditions. However, in the next six weeks of continuous waterlogging most plants died but some clones survived. The survivors were hybrids (except for four 'Narragansett' clones) and this result indicates that survival strongly depends upon a combination of genes from the introduced varieties and the Australian varieties. The contribution of the Australian varieties is possibly winter growth activity and some contribution to tolerance from 'Demnat' and the contribution of the introduced varieties is their greater tolerance to flooding which was evident at Harvest 2 but was not expressed at the final scoring for survival.

The only overall differences between the control and selected groups of clones was in the number of shoots per plant and one visual scoring. However within some populations a number of plant characters differed significantly between the selection groups. These differences were caused by fifteen of the sixty selected clones and there may have been a greater likelihood of obtaining differences between the control and selected groups if superior clones had been selected from a much larger population than that from which the clones were selected at the completion of Experiment 2.

A selection index based on the plant appearance and yield of individual plants during the flooding treatment in addition to their regrowth after flooding may have also increased the likelihood of selecting clones from the survivors of the previous experiment which were more tolerant to flooding. Some of the clones selected only on the basis of their regrowth may have been severely affected during flooding, but retained sufficient living root and crown tissue to initiate new growth when the flooding treatment was removed. Crowns which had higher numbers of active shoot buds when regrowth commenced after flooding would have been favoured during selection.

The clones which survived flooding in this field experiment were growing in flooded and waterlogged soil conditions for three months which is equal to or greater than the period of waterlogging which occurs in most waterlogged areas of southern Australia (except for swampy areas and low-lying depressions). The surviving clones from the experiment can therefore be used as a population from which a waterlogging tolerant and agronomically acceptable variety may be selected.

6. GENERAL DISCUSSION

6.1. The expression of waterlogging tolerance by the varieties and hybrid populations which were studied

In all of the experiments in this study, significant differences in tolerance to waterlogging have been found between parents, hybrid populations and individual lucerne clones.

The eight lucerne varieties used as parents in this study were chosen to include four which had been reported to be tolerant to waterlogging ('Marusinskaya 81', 'Marusinskaya 425','Rhizoma' and 'Narragansett') and four which express agronomic characteristics, other than waterlogging tolerance, considered desirable in Australian agricultural systems and adapted to southern Australia ('Du Puits', 'Hunter River', 'African' and 'Demnat'). These eight varieties also represent a spectrum of ecotypes of the *Medicago sativa* - *Medicago falcata* coeno-specific complex. They range from the extreme "sativa" forms, 'Demnat' and 'African', to 'Marusinskaya 425' which is taxonomically close to *Medicago falcata* and expresses little introgression of characteristics from *Medicago sativa* although, like its sister line 'Marusinskaya 81', it was selected from an interspecific hybrid population (Sinskaya, 1951). 'Rhizoma' and 'Narragansett' also had a common contribution to their parentage from *Medicago falcata* var. 'Don' (Bolton, 1962).

A higher general level of tolerance was expressed by the four introduced varieties, 'Marusinskaya 81', 'Marusinskaya 425', 'Rhizoma' and 'Narragansett', than by the Australian varieties and they contributed this characteristic to hybrids between the two groups of varieties. The four introduced varieties have a common ancestry in the floodland ecotypes of *Medicago falcata*, which is widely distributed in the Caucasus and central European Russia.

The average response of the lucerne populations studied was similar to that of the variety 'Rambler' (Heinrichs 1970, 1972), but the performance of the most tolerant varieties and clones, particularly in the groundwater rendzina soil, was much better than the average performance and approached that of tolerant species of Trifolium (Hoveland and Webster, 1965; Marshall and Millington, 1967; Heinrichs, 1970). Similar intra- and interspecific variation exists in the annual species of the genus Medicago, in which some genotypes of the most tolerant species (M. polymorpha) expressed tolerance comparable to that of the annual clover Trifolium subterraneum.

In all experiments the parents and hybrids generally expressed a consistent pattern of performance, in which the four introduced varieties were the most tolerant, the Australian varieties the least tolerant and the average hybrid performance was intermediate. This pattern only differed in the field experiment in which, immediately after the commencement of flooding, some clones of 'Demnat' were tolerant (in contrast to the extreme sensitivity of 'Demnat' in the glasshouse) and, after prolonged flooding, the introduced varieties did not survive flooding in the winter dormant phase of their growth.

Because the parents and hybrids were heterogeneous and considerable variation within populations was expressed at the clonal level no conclusion can be made on the genetic basis of waterlogging tolerance or the contribution of waterlogging tolerance to the most tolerant hybrid clones. However, the higher proportion of tolerant plants in the introduced varieties when grown in the glasshouse and when initially flooded in the field, suggests that they are the strongest contributors. The persistence of a few Demnat clones during the first weeks of flooding in the field suggests that a component of tolerance to flooded conditions may be contributed by this variety. A proportion of the hybrid clones expressed winter activity as had been previously reported by Morley et al. (1957) for hybrids between dormant and active varieties assessed in a southern Australian environment. Analysis at the clonal level in the field indicated that waterlogging tolerance and winter activity were present in the survivors of prolonged flooding which were almost all hybrid clones. Therefore the adaptation of lucerne to waterlogging under field conditions during the winter in southern Australia requires a combination of genes from the introduced varieties, which contribute strongly to waterlogging tolerance, and also from the Australian varieties, which contribute winter growth characteristics.

The continuous distribution of levels of tolerance within parents and hybrids (Figure 12) and the overall differences in tolerance between soils and environments indicate that tolerance is not controlled by one (or only a few) genes having a major effect but rather by a larger number of genes controlling the expression of many characters. The general lack of significant population x soil (i.e. genotype x environment) interactions under flooding also indicates that there are no specific combinations of genotype and soil which confer specific tolerance (or lack of it) within the range of genotypes and soils which were studied. The only major exception to the above occurred when the two Russian varieties and some hybrid plants expressed little deterioration in plant appearance in the flooded groundwater rendzina soil in Experiment 2. Further selection may therefore be most rewarding in selecting a population adapted to flooded alkaline black earth soils.

6.2. The effect of differences between the glasshouse and field environments on the assessment of waterlogging tolerance

The major differences between the glasshouse and field environments were in the methods of flooding, the temperatures, the daylengths and the soil types.

In Experiments 1 and 2 the flooding treatment was applied by suddenly immersing root systems growing in well-drained aerated soil and maintaining the water level just above the soil surface but in the field flooding did not quickly immerse the root systems. Daily flooding gradually raised the watertable and only after five weeks was the profile waterlogged (Tables 33 and 34).

Therefore plants with root systems able to function in the non-waterlogged but almost completely saturated surface horizon in the first weeks of flooding in the field would have been at advantage but in completely waterlogged conditions this advantage may not have been expressed. The small number of 'Demnat' clones which were tolerant after seven weeks of flooding (only two weeks of complete waterlogging) may have been advantaged by this difference between environments because the adventitious root development, observed during Experiment 2 on the selected clone subsequented found most tolerant at Harvest 2 in Experiment 3, was expressed in the field as a strongly developed mat of roots in the soil surface which was saturated but being daily permeated by oxygenated floodwater. When the site became completely waterlogged these clones died (Table 42) and in the glasshouse experiments no 'Demnat' plants were as tolerant (using visual assessment) as many plants in the introduced varieties when the soils were completely waterlogged.

The mean air temperature in the field (at the nearest meteorological station) was 8.8°C (Appendix 8) and the daylength in June and July is approximately ten hours but the mean glasshouse temperatures during the imposition of flooding were 15.8°C and 19.4°C in Experiments 1 and 2 respectively (Appendices 5 and 6).

These differences in temperature and daylength affected the growth patterns of the parents and hybrids. In the non-flooded treatments in the glasshouse there were only small differences in yield between all populations (Tables 6 and 19) although varietal and heterotic effects were present. However in the field the winter dormancy of introduced varieties and clones within the hybrid populations reduced the average yields of these populations (Table 36). Therefore, in the glasshouse where all populations were growing actively the highest yields occurred in the introduced varieties which were affected least by flooding, but in the field at Harvest 2 'Marusinskaya 81' and 'Narragansett' were winter-dormant and lower yielding than 'Demnat' (Table 38) although they were less affected by flooding when assessed visually (Table 40). The yield of the other Australian variety, 'Hunter River', was not significantly higher after flooding (Table 38) because all clones of that moderately winter active variety (Leach, 1971) had been severely affected by flooding (Fig. 12).

The introduced varieties consistently retained a higher proportion of meristemmatic activity and suffered less decline in plant appearance than the Australian varieties both in the glasshouse (Tables 10 and 29) and in the first seven weeks of flooding in the field (Table 40). The introduced varieties were also more tolerant than the hybrid populations in the glasshouse (Table 29) but in the field the hybrids did not generally differ significantly in appearance from the introduced parents (Table 41) and after prolonged flooding almost all clones retaining meristemmatic activity were hybrids (Table 42). In the field the introduced varieties generally did not regrow after harvest 2 and were severely affected by flooding.

Plant appearance is a more consistent criteria for assessing tolerance than yield, because it is not as sensitive to the environmental influence on plant growth and gave the same general ranking of the parents and hybrids in both the glasshouse and field but assessment in yield is confounded with plant growth. Dormant plants, which cannot be easily scored for appearance or apical activity, were killed by inundation (Table 42) and therefore tolerance of and survival in waterlogged conditions during the winter can be measured by scoring the appearance of plants growing in an environment which permits expression of winter dormancy.

The number of shoots which developed per plant in nonflooded conditions was dependent upon the environment, experimental conditions and the growth of the plants (compare Tables 22 and 36). The greater propensity of the introduced varieties to produce shoots under conditions favouring active growth (Table 23) was not expressed by these varieties while entering a winter dormant growth phase (Table 36). Therefore, as found for yield, there is not a consistent relationship between tolerance, based on plant appearance, and shoot production.

The soil at the field site was most closely related to the solodized solonetz soil used in the glasshouse although it was slightly higher in pH than the solodized solonetz and contained more soluble salts than any soil used in the glasshouse (compare Appendices 4 and 7). The general lack of population x soil interactions in the glasshouse using three diverse soils (Appendices 1,2 and 3) and the similarity of the solodized solonetz soil and the soil at the field site suggest that differences between soils would not have contributed to differences between populations under flooded conditions.

In the diverse range of temperatures, daylengths, flooding conditions, plant densities and soils used in these experiments the most consistent criterion for assessing waterlogging tolerance was the appearance of actively growing plants.

6.3. The morphological and physiological consequences of waterlogging and the expression of adaptive mechanisms

Severe reduction and cessation of rootgrowth accompanied by rotting and disintegration of healthy tissue occurred in almost all plants, corresponding with the results of Rogers (1974), Cameron (1973), Heinrichs (1970, 1972) and Tovey (1964) who found that after flooding for a few days the roots of lucerne were seriously damaged. Rapid necrosis and rotting within a few hours at high temperatures, which had been observed by Cameron (1973) and Lehman et al. (1959) did not occur in this series of experiments.

Morphological adaptation to flooding occurred in some plants on which short, less branched fibrous roots developed from the crown near the soil surface. Although this root development was weak it is possibly a morphological adaptation similar to adventitious root development in other species (Valoras and Letey, 1966; Jackson, 1955). These roots were not obviously noticable until two or three weeks after flooding when they were associated with plants retaining meristemmatic activity and healthy, but retarded, shoot growth. In Fig. 6 the representative plants of Marusinskaya 425 (M425) and Narragansett (N) illustrate the presence of a fibrous root system which arose from near the crown on those plants. Thick less-branched adventitious roots were observed during flooding in Experiment 2 on the 'Demnat' clone which was subsequently included in the field experiment and expressed the highest tolerance after seven weeks of flooding. The slower rise of the watertable and soil water content in the field may have allowed a stronger development of these roots in some 'Demnat' clones than would have been permitted by the sudden immersion of root systems in the glasshouse. Sudden hydrological changes can even disrupt growth in more tolerant species cultivated in waterlogged conditions (Varade, Letey and Stolzy, 1970).

Nodules were observed on the surface and adventitious root tissue of some plants in both the glasshouse and field. I have observed a similar distribution of nodules on waterlogging tolerant Trifolium species. The retention of some active nodules by lucerne would compensate for the loss of nitrogen fixation by nodules within the waterlogged soil. The oxygen and nitrogen demands of nodules must be met to permit them to continue functioning (Bergersen, 1971). The dissolved oxygen and nitrogen in the surface layer of the waterlogged treatments seemed adequate for nodule activity but nodules deeper in the waterlogged zones disintegrated and were lost. Because nodule activity depends upon the presence of healthy supportive root tissue, the rotting of roots and absence of adventitious roots most plants would not have allowed nodule survival or development, and therefore possibly restricted the expression of nodule activity.

Partial desiccation of plant tops occurred in all populations (Table 8) and suggests a detrimental effect of flooding to some degree in all varieties.

The exclusion of oxygen from roots probably reduced water absorption and the transpiration rate as reported in other species (Letey, Lunt et al. (1961); Willey (1970); Kramer and Jackson, (1954)).

Continued flooding, causing permanent root damage, would have also reduced the potential uptake of water.

The yellowing of apices and early symptoms of flooding damage were similar to those reported by Graven et al. (1965) which they correlated with manganese accumulation. An adaptive mechanism similar to that reported by Ouellette and Desureaux (1958b), in which manganese translocation was lower in tolerant clones particularly in the presence of calcium, may have contributed to the high tolerance to flooding of some plants growing in the alkaline groundwater rendzina soil (Figure 10).

The death of winter dormant clones in the field after prolonged flooding contrasted with the survival of winter active hybrids (Table 42) and suggests that an important adaptive mechanism of lucerne to flooding is the maintenance of growth so that the plants avoid inundation. Bendixen and Peterson (1962) have found that a tropism in *Trifolium fragiferum* which keeps leaf tissue above the surface of the water in flooded treatments is a major adaptive mechanism.

In lucerne this mechanism is provided by the erect growing shoots of the hybrids which are above and do not lie in the shallow free surface flood water.

6.4 Selection of a waterlogging tolerant lucerne variety which is agronomically suitable for southern Australia

In the two glasshouse experiments the most tolerant plants occurred in the four introduced varieties, but in the field the most tolerant after prolonged flooding generally occurred within hybrid populations.

Although surviving plants which retained meristemmatic activity occurred within the Australian varieties during the glasshouse experiments (Tables 10 and 30) these surviving plants were more affected by flooding than the most tolerant plants of the introduced varieties and had an appearance similar to scores 4 and 5 (Figure 8) whereas the most tolerant plants had scores of 2 and 3 (Figures 7 and 10). In the field at harvest 2 some Demnat clones had scores for plant appearance as low as clones of the introduced varieties (Figures 11 and 12) but subsequently they deteriorated.

Selection in the glasshouse experiments for both minimal plant deterioration and yield would have therefore resulted in the choice of plants from the introduced varieties and in the first weeks of flooding in the field selection would have favoured clones of 'Demnat' and some hybrid clones, but none of these populations provided the most tolerant clones. After prolonged flooding the selected clones would have been chosen from hybrids (Table 42).

In this study the hybrid populations were generated by randomly crossing unselected parent plants, but variation in tolerance exists within all the parental populations (Fig. 12) and selection of the most tolerant clones to use as parents may increase the frequency of tolerant hybrids within their progeny.

Selection within the glasshouse permits a close control of the flooding treatment from which plants which maintain meristemmatic activity and express surface root development may be selected but the yields obtained in the glasshouse, particularly under higher temperatures and longer days than those of field conditions in winter, are not reliable and yield assessment must be done in the field to discriminate between winter-dormant and winter-active hybrids. Gradually increasing the soil water content and raising the watertable in the glasshouse to more closely simulate the field situation may also result in an improved selection of both parental clones and tolerant hybrids. In the field care must be taken to ensure that flooding is applied uniformly on the selection site because small differences in the relation of the free water surface to the soil surface can be reflected in quite large differences in plant performance as demonstrated by the decline in plant appearance of all populations in Experiment 3 when the soil profile became completely waterlogged (Table 40).

Although there were few population x soil interactions in the glasshouse experiments, the effect of flooding was generally significantly less in the groundwater rendzina soil and the Russian varieties were significantly more tolerant (when assessed visually) in that soil and therefore a population having tolerance sufficient for adaptation to the groundwater rendzina soils may be more easily obtained than for the sites from which the solodized solonetz and lateritic podsol soils were chosen.

In southern Australia lucerne is utilized as a pasture and fodder plant at all times of the year. The growth rhythms of the introduced varieties in this study would reduce herbage yields from late autumn to early in spring. Although this loss could be compensated by growth of companion species which are more winter active e.g. cultivars of the grasses *Lolium perenne*, *Lolium multiflorum*, *Phalaris tuberosa* and *Festuca arundinacea* or by the clovers *Trifolium subterraneum*, *Trifolium fragiferum* and *Trifolium repens* , I have observed that the dormant lucerne crowns tend to reduce the total herbage yield by competition for ground cover. In addition, because extremely dormant clones were killed by flooding, it would be necessary to retain as much winter vigour as possible in waterlogging tolerant selections. The tolerance of lucerne to summer drought, its growth in late spring and summer when many other pasture species are more affected by moisture stress, and its suitability for forage harvesting and production of high quality hay are strong agronomic reasons for attempting to extend the utilization of lucerne in southern Australia into areas from which current varieties are excluded because they are not adapted to the period of winter waterlogging.

The introduced varieties do not have a seed yield as high as the Australian varieties (Appendix 9).

To breed a waterlogging tolerant lucerne variety, selection must be made during the programme for both waterlogging tolerance in a range of soils and for other agronomic requirements, particularly seed production, summer yield and adaptability to management practices.

Using a modification of the technique employed in this study to more closely simulate field flooding, tolerant clones of both the introduced and Australian varieties could be obtained in initial selection in the glasshouse, by assessing actively growing plants using a visual score.

From field assessments of hybrids between individual clones from both the introduced and Australian varieties at a number of sites, tolerant hybrid clones could be selected. I have found that the frequency of F_1 hybrid clones having an acceptable seed yield is lower than the frequency of winter active clones in crosses involving the extremely winter-dormant introduced varieties in this study. Therefore another cycle of hybridization between the tolerant F_1 clones (or alternatively a backcross of the tolerant F_1 clones to the Australian parents) followed by selection for tolerance may increase the frequency of segregants in which waterlogging tolerance and acceptable seed and herbage yields are combined.

From these segregants elite clones could be chosen by comparing replicated clonal propagules in a number of waterlogged sites and in trials designed to measure their potential yields of herbage and seed and adaptability to management practices.

Further cycles of hybridization and clonal assessments may be required.

From a comparison of polycross or diallel progenies produced from the clones selected after the final cycle of hybridization a small number of parent clones for a synthetic variety could be selected. The performance of the progenies and their stability from site to site would indicate whether it is possible to synthesise one cultivar having a wide adaptation or, alternatively, cultivars for specific environments.

This study of the variation in waterlogging tolerance of lucerne has demonstrated the value of hybridization between local varieties which do not express tolerance and introduced varieties which are less affected by waterlogging but which are otherwise poorly adapted. The experiments in the glasshouse defined the range of variation in waterlogging tolerance and its expression in intervarietal hybrids. In the contrasting field environment the survival of some plants from these hybrids has provided encouraging evidence that the breeding of a waterlogging tolerant lucerne which is adapted to southern Australia should be pursued.

APPENDIX 1.

Description of the Solodized Solonetzic Soil from the Kybybolite Research Centre, South Australia.

(exert from 'A Handbook of Australian Soils', by Stace et al., (1968), pp 172-173)

Location: South-east district, South Australia; 36°54'S., 140°56'E; 330ft. (101 m).

Topography: Undulating plain with local relief of 30ft. (9m). Site on a gentle, west-facing slope.

Climate: Kybybolite, 36°53'S., 140°55'E; 299ft. (91 m). Evaporation: 44in. (1,120mm). Rainfall: 20in (510 mm); winter maximum.

Temperature: Jan. 82°F., 50°F. (28°C., 10°C.); July 56°F., 39°F. (13°C., 4°C.).

Parent Material: Quaternary sandy clay or clayey sand.

Profile Drainage: Impeded by clay subsoil.

Native Vegetation: Cleared. Originally savannah woodland. Remaining trees, mainly Eucalyptus camaldulensis (red gum) and E. leucoxylon South Aust. blue gum).

Land Use: Kybybolite Research Centre: Sheep and cattle grazing on improved pastures.

Morphology:

No.	Depth		Description
	in.	cm.	
1a	-2	-5	Greybrown (10YR 4/2 moist); sandy loam; weak crumb; soft, mellow (moist). Some fine roots. Moderately sharp to -
1b	-4	10	Grey-brown (10YR 4/2, 5/4 dry) flecked with yellowish brown and light grey; sandy loam; massive; moderately compact. Some fine roots. A little hard, subangular, uniform ferruginous gravel ($\frac{1}{4}$ in., $\frac{1}{2}$cm.) of cemented quartz grains. Diffuse to -

APPENDIX 1. (Continued)

Morphology:

No.	Depth		
	in.	cm.	
2	-8	-20	Very light brown (10YR 8/2 dry, 7/3 moist) flecked with (10YR 5/3); loamy sand; massive; moderately compact. A few fine roots. Much ferruginous gravel. Sharp to-
3a	-10	-25	Mottled dark red (10R 3/6), dark grey-brown (10YR 3/2); clay with veins and pockets of offwhite (10YR 8/2) sand; broad columnar (6in., 15cm.), breaking to prismatic with polished clay skins on ped faces; tough. Bleached sand and ferruginous gravel adhere to uneven tops of columns. Arbitrary to -
3b	-12	-30	Similar to 3a above, but with less included sand and breaking to angular cloddy. An occasional piece ferruginous gravel. Arbitrary to -
4a	-16	-40	Similar to 3b above at the top, changing in colour with depth to red-brown (5YR 4/6) and grey-brown (5YR 4/2). Merging to -
4b	-20	-50	Similar to 4a above, except that the colour is reddish brown (5YR 4/4) diffusely mottled with dark grey (5YR 4/1). A little ferruginous gravel. Merging to -
4c	-24	-60	Yellowish brown (7.5YR 5/6) with some of the ped faces somewhat darker; clay; columnar, breaking to prismatic with clay skins less noticeable; friable. Occasional piece ferruginous gravel. A little soft carbonate from 21 in. (52 cm.). Arbitrary to -
5	-35	-90	Yellow-brown (7.5YR 5/6); clay; massiv; friable. Occasional piece ferruginous gravel. Some soft carbonate in cone-like pickets.

APPENDIX 2.

Description of the Groundwater Rendzina soil from the Maaooze Soil Association, South Australia. (Extracted from C.S.I.R.O. Div. of Soils, Rep. 4/65 Clarke (1965), p. 110)

Profile 114	Ground Water Rendzina.
Location	County Robe. H^d Robertson. On road reserve between Sections 160 and 327. Approx 5 chains N of SE cnr Section 160, approx. 5 yards from E side of road reserve.

Morphological Description

0-3 in.	Black (moist) - dries to very dark grey - silty clay loam. Granular and crumbly. Many roots. Low carbonate.
3-6 "	Black (moist) clay granular and crumb - friable but slightly compact. Low carbonate.
7-12 "	Very dark grey (moist) granular clay. Increasing carbonate. Heavy limestone being weathered.

Soil No.	Depth in.	Grav %	pH	T.S. %	NaCl %	Ign Loss %	Moist %	Nit %	Org C %	Phos %	Pot %	Carb. %	CS %	FS %	Si %	Cl %
A675/1	0-3		8.4	.079	.023	15	9.0	.45	5.8	.026	1.6	5.7	2	23	9	49
/2	3-6		8.6	.097	.028	14	9.6	.35				9.2				
/3	7-12	71	8.9	.17	.054	17	8.2					21	1	20	4	52

APPENDIX 3.

Description of the Lateritic Podsol soil from the Second Valley Forest, South Australia.

(Clarke A.R.P. personal communication)

Depth	Boundary	Colour	Texture	Structure	Consistence
0-1	diffuse	10YR3/1 (moist)	L c.o.m.	crumb	friable
1-8	Diffuse	10YR5/4 (moist)	L	v. weak crumb	friable
8-16	Diffuse	10YR5/8 (moist)	C	dense	friable
16-32	Diffuse	Mott 7.5YR5/8, 10YR5/8 10YR6/4 2.5YR3/4	C &	dense massive laterite	
32-58	Diffuse	Coarse mott. 10YR7/2 5YR4/6, 7.5YR5/6	C	angular blocky	hard

APPENDIX 4.

Laboratory Analysis of Soils Used in Experiments 1 and 2.

Soil 1: Solodised Solonetz

Depth (cm.)	Total Soluble Salts (%)	pH	Mechanical Analysis			
			% Gravel	%Sand	% Silt	% Clay
0-8	.018	6.7	3	85	8	4
8-13	.009	6.8	10	77	5	8
13-20	.012	7.2	29	61	6	4
20-31	.015	7.2	50	41	4	5
31-51	.040	8.1	6	30	4	60
51-66	.050	8.6	2	50	1	57
66-90	.101	9.1	2	51	2	45

Soil 2: Groundwater Rendzina

0-6	.062	7.7	0	36	7	57
6-31	.059	7.9	0	23	11	66
31-36	.102	8.5	58	9	5	28
36-60	.125	8.7	81	9	3	7

Soil 3: Lateritic Podsol

0-8	.019	7.6	36	44	8	12
8-15	.012	7.5	39	35	9	17
15-20	.013	7.0	52	30	6	12
20-38	.018	6.6	31	28	6	35
38-48	.015	6.1	64	9	3	24
48-61	.015	5.9	64	4	3	29
61-69	.015	5.8	72	7	1	20
69-76	.015	5.6	77	6	2	15
76-81	.015	5.7	74	6	3	17
81-90	.016	5.7	66	6	3	25

APPENDIX 5.

The minimum, mean and maximum daily temperature and humidity during the period of flooding treatment in Experiment 1.

Date	Days of Flooding	Temperature			Humidity		
		min.	mean	max.	min.	mean	max
June 23	0	12.0	16.0	20.5	46	50.5	55
24	1	11.5	15.5	20.0	39	47.5	56
25	2	11.0	17.0	22.0	37	46.5	56
26	3	10.5	15.5	20.5	50	60.5	71
27	4	12.0	17.0	21.0	32	49.0	66
28	5	11.0	14.5	18.5	47	59.5	72
29	6	11.0	16.0	21.0	47	59.0	71
30	7	10.5	14.5	19.0	51	63.5	76
July 1	8	12.0	17.0	23.0	51	61.0	71
2	9	12.0	17.0	21.0	60	65.5	71
3	10	10.5	15.0	19.5	51	62.0	73
4	11	12.0	17.0	21.0	41	56.5	72
5	12	12.0	17.0	23.0	47	61.5	76
6	13	12.0	16.0	20.5	48	62.0	76
7	14	11.5	17.0	21.5	47	58.0	69
8	15	10.0	14.0	18.5	55	64.0	73
9	16	11.5	13.5	15.0	56	63.0	70
10	17	12.0	15.5	19.0	58	67.0	76
11	18	12.0	17.0	21.0	57	68.5	80
12	19	12.0	14.5	17.0	64	74.5	85
13	20	13.0	16.0	20.0	49	59.5	70
14	21	12.0	15.5	19.0	48	57.0	66
15	22	11.5	16.0	20.5	52	59.5	67
16	23	13.0	14.5	16.5	60	68.5	77
17	24	12.0	15.0	18.0	66	72.0	78
18	25	12.0	16.0	20.0	36	51.0	66
19	26	11.5	15.5	20.0	48	58.0	68
20	27	11.5	15.5	19.5	49	59.0	69

APPENDIX 5. (Continued)

Date	Days of Flooding	Temperature			Humidity		
		min.	mean	max.	min.	mean	max.
July 21	28	13.5	17.0	20.0	60	68.0	76
22	29	13.0	17.0	22.0	54	64.5	75
23	30	12.0	17.0	22.0	47	56.5	66
24	31	12.0	15.5	19.5	50	60.5	71
25	32	11.5	16.0	21.0	59	60.5	71
26	33	12.0	15.0	18.5	51	60.0	69
27	34	12.0	17.0	21.0	45	50.5	56
28	35	12.0	16.0	20.5	44	51.0	58
29	36	11.5	16.0	21.0	45	53.0	61
30	37	12.0	15.0	18.0	41	50.5	60
31	38	11.5	13.5	15.5	39	50.5	62
August 1	39	11.0	15.0	19.5	47	59.0	71
2	40	11.0	17.0	24.0	45	59.5	75
Mean over the experimental period		11.72	15.79	19.96	49.2	59.3	69.4

APPENDIX 6.

The average weekly minimum, maximum and mean temperatures and humidities during establishment, flooding and regrowth in Experiment 2.

Week Commencing	Temperature (°C)			Relative Humidity (%)		
	Min.	Max.	Mean	Min.	Max.	Mean
Establishment Period						
January 31, 1974	18.3	23.5	20.9	70.2	96.2	83.2
February 7	17.8	23.6	20.7	79.4	96.0	87.7
February 14	16.7	22.9	19.8	75.0	92.5	83.8
February 21	16.7	27.4	22.1	64.7	89.0	76.9
February 28	20.7	29.5	25.1	66.6	92.7	78.7
March 7	16.7	25.1	20.9	74.3	94.1	84.2
March 14	17.5	25.1	21.3	72.3	93.3	82.8
Mean	17.8	25.3	21.5	71.8	93.4	82.8
Flooding Period						
March 21	17.4	24.6	21.0	74.9	92.0	83.4
March 28	18.1	24.8	21.5	67.6	90.6	79.1
April 4	14.4	21.0	17.7	75.4	94.3	84.9
April 11	14.4	22.7	18.6	66.3	91.1	78.7
April 18	16.7	22.8	19.8	74.1	93.1	83.6
April 25	14.1	21.9	18.0	66.6	93.0	79.8
Mean	15.9	23.0	19.4	70.8	92.4	81.6

APPENDIX 6 (Continued)

Regrowth Period						
May 2	15.2	22.8	19.0	67.9	89.4	78.7
May 9	14.3	25.3	19.8	63.4	93.8	78.4
May 16	9.3	19.4	14.4	57.4	90.4	73.9
May 23	6.6	23.5	15.0	52.6	86.3	69.4
May 30	10.7	20.8	15.8	58.7	88.3	73.5
June 6	10.2	22.4	16.3	63.3	87.4	75.4
Mean	11.1	22.4	16.7	60.6	89.3	74.9

APPENDIX 7.

Laboratory Analysis of the soil profile from the field site used in Experiment 3.

Depth (cm.)	Total Soluble Salts (%)	pH	Mechanical Analysis			
			% Gravel	% Sand	% Silt	% Clay
0-8	0.184	7.2	0	67	23	10
8-14	0.110	7.5	0	69	21	10
14-27	0.070	7.6	0	62	27	11
27-33	0.068	7.7	6	48	27	19
33-64	0.144	7.5	0	15	60	69
64-91	0.146	6.7	0	23	24	53

APPENDIX 8.

The average weekly minimum, maximum and mean air temperatures at Mount Barker, South Australia, during the periods of growth before Harvests 1 and 2 in Experiment 3.

Week Commencing	Temperature (^{o}C)		
	Minimum	Maximum	Mean
Before Harvest 1			
April 30, 1975	7.0	18.7	12.9
May 7	10.4	16.7	13.6
May 14	11.0	16.1	13.6
May 21	10.7	18.3	14.5
May 28	7.9	17.1	12.5
Means	9.4	17.4	13.4
Before Harvest 2			
June 4	3.1	16.1	9.6
June 11	3.4	12.3	7.9
June 18	0.3	12.3	6.3
June 25	5.7	14.1	9.9
July 2	3.3	13.4	8.4
July 9	6.6	13.6	10.1
July 16	4.6	13.7	9.1
Means	3.9	13.6	8.8

APPENDIX 9.

The average yield (gm per plant) of thirty spaced plants of each of the eight parent varieties at Northfield, South Australia, during 1974 - 75.

Variety	Seed Yield
Marusinskaya 81	1.0
Marusinskaya 425	0.3
Rhizoma	10.1
Narragansett	8.1
Du Puits	15.6
Hunter River	30.9
African	22.0
Demnat	21.2

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