THE UNIVERSITY OF MANITOBA

LIBRARY

AUTHOR ...WIEBE, Theodore John.....

TITLE ....WATER-TEMPERATURE INTERACTIONS IN GERMINATIONS AND DORMANCY IN WHEAT

.....

.....

THESIS ...M.Sc., 1983.....

I, the undersigned, agree to refrain from producing, or reproducing, the above-named work, or any part thereof, in any material form, without the written consent of the author:

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

.....

WATER-TEMPERATURE INTERACTIONS IN GERMINATION AND DORMANCY IN WHEAT

by

Theodore John Wiebe

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Plant Science
The University of Manitoba

Winnipeg, Manitoba, 1983

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read a Master's thesis entitled: ...WATER-TEMPERATURE INTERACTIONS IN GERMINATION AND DORMANCY IN WHEAT

submitted by ...Theodore John WIEBE

in partial fulfillment of the requirements for the degree of

.....MASTER OF SCIENCE.....

The Thesis Examining Committee certifies that the thesis (and the oral examination, if required) is:

Approved [X] Not Approved [ ]

E.J. Woodbury

Advisor

E. Shaykewich

Ian Morrison

.....

.....

External Examiner

Date .....August 8, 1983.....

.....

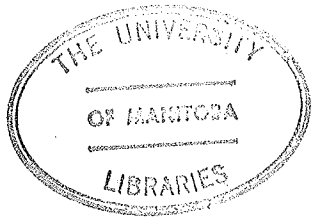
WATER-TEMPERATURE INTERACTIONS IN GERMINATION AND DORMANCY IN WHEAT

BY

THEODORE JOHN WIEBE

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE



ACKNOWLEDGEMENTS

I would like to thank everyone who assisted me in this thesis project, especially Dr. Bill Woodbury whose guidance, many ideas, and friendship were a constant encouragement; Dr. Ian Morrison and Dr. Carl Shaykewich for reading the manuscript; Larry Sernyk for statistical and computer help; Rick Zillman, Bert Luit and John Waterer for their technical help; and my sister Irmie for a fine typing job.

ABSTRACT

Wiebe, Theodore John M.Sc., The University of Manitoba, 1983. Water-Temperature Interactions in Germination and Dormancy in Wheat.

Major Professor: Dr. William Woodbury, Department of Plant Science.

Water uptake and germination of wheat was examined at various temperatures, water availabilities, and positions, using various kinds of seeds. All experiments were conducted in temperature-controlled lab conditions. External resistance to seed water entry was achieved by placing seeds on moist sand or using vapour phase uptake. Non-dormant, post-harvest dormant, and coumarin treated seeds were examined. Various seed orientations on the sand, and dye uptake were used in controlling and determining location of entry.

Higher sand hydraulic conductivity resulted in reduced germination time as well as increasing germinated seeds' water content in warmer temperatures. Increased seeding densities or larger seeds depleted more sand water prior to germination. Hence greater decreases in hydraulic conductivity occurred, delaying germination. Non-dormant

seeds which contacted liquid water germinated very rapidly, as was the case when the embryo seed ends contacted moist sand. Increased temperatures decreased germination time primarily by decreasing the lag period. With warmer temperatures, the decrease in germination time was not as great in post-harvest dormant seeds, possibly due to slower water uptake compared to non-dormant seeds. The spring wheat Neepawa germinated slower than the winter wheat Norstar, apparently due to higher water requirements. Vapour phase studies showed two distinct phases of uptake prior to germination. Cold temperatures prevented seeds from germinating in the vapour phase. Coumarin-treated seeds behaved similarly to dormant seeds in that strong germination inhibition was only pressent if seeds contacted liquid water. In one sample of dormant seeds strong inhibition of germination occurred when only the brush end of seeds contacted moist sand. The dye experiment showed frequent uptake at the brush region and subsequent movement under the pericarp to the embryo, suggesting a route for pericarp inhibitors to the embryo.

TABLES

FIGURES

CONTENTS

Chapter I

INTRODUCTION

Seeds of most plant species usually display some degree of dormancy at maturity. Dormancy is a safety control mechanism allowing a seed to exist at an extremely low metabolic state over a time period where environmental conditions possibly cannot support the active vegetative phase of that plant. Upon the arrival of more favourable conditions and the elimination of dormancy, a viable seed should germinate.

Dormancy generally refers to a seed's inability to germinate, even though conditions conducive to germination are present. Dormancy may be both beneficial or detrimental from an agronomic perspective. High sprouting resistance is necessary in minimizing quality losses of mature cereals when harvest is delayed due to moist conditions. Dormancy on the other hand is detrimental to both growers and malsters, in that delayed less-uniform germination will result in an uneven stand for the farmer, and a slower, lower-yielding malt for the malster.

The seeds[1] of cereals have varying levels of dormancy at maturity depending on genetic and environmental characteristics. This dormancy may be due to chemical inhibitors found in the seed, or it may involve physical or structural characteristics. Generally, dormancy diminishes with time, due to leeching out and/or a breakdown of inhibitors and/or structural alterations which make the seed germinable.

It is possible to argue that water conditions and temperature play vital roles in influencing or controlling both kinds of dormancy. It is easy to realize that water will effect both the inhibitor and structural types of dormancy, as large amounts enter the seed. The rate and location of entry as well as movement within the seed could influence dormancy and germination. The influence of temperature on germination could involve membranes, enzymes, and structural polymers, and could interact with water in exerting its effect. Water and temperature may behave as subtle control mechanisms contributing to the control of germination and dormancy. This control may be advantageous from an ecological perspective, but not necessarily from an economic perspective of the grower, miller, or malster.

---

[1] The botanically correct definition of a wheat kernel is a caryopsis, as it is a one-seeded fruit. The presence of the ovary wall or pericarp prevent it from being a true seed. However, since caryopsis are commonly referred to as seeds, this term will be used.

Germination is the beginning of the vegetative stage of the plant life cycle. It results from living seeds taking up water, and becoming metabolically active. Various enzymes such as alpha-amylase and protease break down stored reserves which provide energy to the growing embryo. Due to its growth, the embryo ruptures the seed coat, by pushing usually the radicle first and then the pumule. The precise definition of the actual time of germination varies, as it involves many stages, both non-visible and visible. In this thesis, germination is said to have occurred once the radicle has penetrated the seed coat and becomes visible.

Wheat germination occurs over a fairly wide temperature range. Peterson (1965) stated that effective germination occurred at temperatures ranging from a minimum of 3.5 to 5.5 C to a maximum of 35 C with optimal conditions occurring between 20 and 25 C. Weak germination occurred outside this range to temperatures as low as 0 C and as high as 40 C. The peak germination rate occurred at the optimum temperatures.

Soil water potential influences the supply and rate of water uptake by seeds. Generally lower potentials decrease the germination rate (Bewley and Black, 1978). A very high water potential near 0 may delay germination due to a lack of oxygen associated with water sensitivity (Essery et al. 1955). Owen (1952) determined that wheat could germinate at potentials as low as -20 bars.

There appears to be some interaction between temperature and water potential. de Jong and Best (1977) demonstrated that in wheat the minimum temperature for emergence decreased from 1.3 to 0.2 C when the water potential dropped from -1/3 to -10 bars. They suggested that under dry soil conditions, the seed compensated for this adverse condition by decreasing the "normal" minimum temperature.

Virtually all of the germination studies involving inhibitors have been conducted at lab temperatures (20 degrees) and on wet filter paper (high hydraulic conductivity and water potential close to 0 bars). Soil temperatures between seeding and the seedling stage generally are much lower and water potential, although variable, would generally be below 0 bars. The hydraulic conductivity of the soil as well would limit water movement toward the seed. An understanding of interactions between temperature, seed water uptake rates and locations, as well as seed structure are necessary in controlling and exploiting post-harvest dormancy.

These studies began in response to the question: "Could we treat seeds with a germination inhibitor to allow fall planting?" A brief review of the literature indicated that most studies on seed dormancy, whether natural or induced, have been carried out on wet filter paper at 20 C. The field conditions involved in fall planting and subsequent germination in the spring would include lower temperatures plus lower water potentials and hydraulic conductivi-

ties than the usual laboratory experiment. Preliminary experiments by J. Waterer, R. G. Berard and W. Woodbury had already indicated that coumarin only inhibited the germination of wheat when the seeds were in contact with liquid water. These studies also showed that once germination was initiated, low temperature and water potential had little effect on the slop of the germination curve. These findings suggested that there were strong interactions between temperature and water content, which were influencing water relations and germinability of seeds that were not explained by existing theories. A review of relevant literature carried out by W. Woodbury in areas of cereal chemistry and polymer theory, revealed the fact that polymer theory predicts and experiments confirm that the interaction between solvent and polymer must display two critical temperatures for polymer swelling. Since the endosperm of mature wheat grains is a complex mass of polymers in a non-living structure, the hypothesis developed that competition between the non-living endosperm and the living embryo and aleurone layer for water might be a factor in regulation of germination and dormancy.

The experiments used moist sand as a germination medium in order to limit the hydraulic conductivity external to the seed in the hope that the effects of temperature and water availability on water absorption and germination of seeds might be better defined.

Chapter II

LITERATURE REVIEW

2.1 SOIL WATER RELATIONS

2.1.1 Soil Water Movement

Water movement occurs as the result of a water potential gradient, and moves from high potentials to low potentials. Air dry wheat seeds have been reported to have a water potential of less than 1000 bars (Shaykewich, 1973), whereas soil under field conditions generally has a water potential in the range between field capacity (about -0.1 bars) to the permanent wilting point (about -15 bars). It therefore becomes evident that water moves toward the seed regardless of field conditions. Depending on the water potential and the characteristics of the soil, there may or may not be enough water entering the seed to cause it to germinate.

Water movement encounters resistance in soils, especially at lower water potentials. When water is removed from a soil, the larger pores are the first to lose water. Movement through air-filled pores is slow since vapour phase transfer is a lot slower than liquid transfer. Therefore, water must move in the smaller pores which still contain water, or via the liquid layer which is tightly bound to soil

particles. The tortuosity is greater under these conditions. The path in which the liquid water must travel becomes twisted and greater in distance, so that it takes considerably longer to reach its final destination. A reduction in the radius of a pore by one half results in a four-fold reduction in the velocity of water going through it (Poiselle equation), causing a great increase in the resistance of water flow (Brady, 1974).

Hydraulic conductivity is a term which refers to the rate with which water moves through a soil and it is inversely related to the soil resistance. It is usually expressed in cm/day. The hydraulic conductivity of a soil at a given water potential is dependent upon the character of that soil, especially its particle size distribution. Hydraulic conductivity drops rapidly with a drop in soil water potential. In both sandy and clay soils, hydraulic conductivity is high near 0 bars. Reductions in water potential cause a great decline in sands.

The decline in conductivity of clays is more gradual (Brady, 1974). The hydraulic conductivity of Superstition sand drops approximately five orders of magnitude with a drop in matric potential from 0 to -15 joules/kg. (Taylor and Ashcroft, 1972).

2.1.2 Effect of water potential on germination

Many germination studies have been conducted examining the effect of water potential on germination (Pawlowski and Shaykewich, 1972; Hegarty and Ross, 1978; Bewley and Black, 1978). Generally, the germination rate decreases as water potential decreases, and has some lower limit. Even though wet conditions are conducive to rapid seed imbibition and germination, these conditions may depress germination due to a lack of oxygen (Essery et al. 1955).

In soils with critically low water contents, if soil temperatures fluctuate, the seeds may get adequate water and therefore germinate. When temperature remains constant, uptake may not be sufficient to allow for germination (Hegarty, 1972). This is likely due to water vapour condensing on seeds and being taken up.

2.1.3 Non-soil germination using filter papers or osmotic solutions

Defining the precise soil conditions at any given time is difficult, except under very wet conditions. At negative water potentials, both the matric and osmotic potentials which comprise the water potential are not constant and homogeneous throughout the soil as the seed imbibes water and germinates (Hadas, 1977). The sphere of soil around the seed will tend to become drier than the rest of the soil, resulting in a drop in hydraulic conductivity around the seed. Artificial means have been developed to allow a

more definite control of water potential, but these are not perfect because they lack the characteristics common to soils such as contact area and hydraulic conductivity.

Many water uptake/germination studies have been conducted avoiding soil as an uptake medium, and using wet filter paper and/or osmotic solutions in supplying the seed with water and controlling the water potential (Khan, 1977; Bewley and Black, 1978). In the case of filter paper, enough solution is usually added so that the paper essentially acts as a wick, ensuring that hydraulic conductivity is not limiting. If pure water is used, the water potential is essentially 0 bars. Peterson and Cooper (1979) condemned the filter paper method commonly used, concluding that the creation of uniform hydraulic conductivity and water potential below zero was impossible.

Osmotic solutions also have their short-comings. Even though water potential can be reliably controlled, in both filter paper experiments and experiments in which the seeds are submersed, hydraulic conductivity is not really limiting. Moreover, if the seeds are submersed, the contact area is not limiting as it might be in a soil. Some of the osmotica currently used, such as mannitol or low molecular weight polyethylene glycol solutions may enter the seed, further complicating matters.

Manohar (1966) examined pea germination using various osmotic systems, and argued that the percent germination

is affected by differential permeability and toxicity of the solute. Mannitol, glycerol, and NaCl may enter the seed with little restriction through the micropyle. NaCl exerts toxic effects on germination.

Bassiri, et al. (1977) noticed that the percent germination varied with the type of osmotic substrate used at similar osmotic potentials indicating that the substance itself somehow affected germination. In a solution, diffusion of the solute will be slower than diffusion of water. Hence, as the seed imbibes water, the solute concentration may increase adjacent to the seed.

Membranes have been used to separate the osmoticum from the seed or soil in some studies (Pawloski and Shaykewich, 1972; Shaykewich and Williams, 1971b), thereby eliminating some of these problems. The membrane is to be semipermeable allowing only water to pass through it. Problems may occur in lengthy experiments in which membrane integrity may deteriorate due to microbial attack. Moreover, Shaykewich and Williams determined that the membrane had a measurable hydraulic conductivity. This might affect results, especially when the water potential of the osmoticum is high, in which case the membrane could become the limiting factor.

Thill et al. (1979) reported considerable variations in water potential of similar concentrations of polyethylene glycol from different lots. Manufacturers put the approximate molecular weight on the package, but there may

be considerable variation within a given lot. Given that there are significant differences between lots, each lot should be calibrated separately in determining the concentration water potential relationship. Thill also noticed a slight decline in the osmotic potential of dilute PEG with time, indicating that it is not entirely stable.

2.2 SOIL-SEED INTERACTION

2.2.1 Effect of contact area, seed size, and seeding density on imbibition

Contact area between the seed and the medium has been documented to have an effect on the uptake rate (Sedgley, 1963; Collis-George and Hector, 1966; Shaykewich and Williams, 1971b). With more of the seed in contact with liquid water, uptake will be greatly enhanced. In the case of soils, liquid water is bound to soil particles. Therefore the better the contact with soil particles, the better the uptake. Some soils which shrink upon drying, such as the 2:1 clays, may experience poor contact as the soil moves away from the seed leaving only a minimal contact area. Harper and Benton (1966) showed that seeds which excrete a mucilage have better water uptake success than non-mucilage excreting seeds, especially under drier soil conditions. The mucilage essentially acts as a wick, enlarging the seed's sphere of influence.

Hadas (1977) examined the effects of seed size and soil aggregate size relative to contact area. He concluded

that contact area was not that important if the seed size to soil particle size ratio is large, and seeds were in the soil rather than on the surface. Seeds tended to take up more water if the soils had smaller particles.

Muchena and Grogan (1977) studied the effects of corn (Zea mays) seed size on germination in a mannitol solution. Contact area was never limiting, yet smaller seeds germinated more rapidly, especially when under stress. Smaller seeds have a lower total water requirement for germination, and also have a greater surface to volume ratio, accounting for the more rapid germination.

Seeding density has been demonstrated to affect uptake patterns. Shaykewich and Williams (1971b) using rapeseed placed on soil, reported that despite identical contact areas and initial water potential, the sparsely placed seeds took up water more rapidly. The sparsely placed seeds could take up water from the hemisphere of soil below and around it, whereas the densely placed seeds were restricted to taking water only from the soil directly below it. The densely placed seeds not only had a smaller volume of soil to draw water from, but the hydraulic conductivity became limiting sooner, since the soil became drier faster.

Harper and Benton (1966) studied the water relations of seeds placed on the surface of a medium rather than within it. Under conditions where the relative humidity was under 100%, the seed would only germinate if the amount of wa-

ter entering the seed from the medium below was greater than the amount lost into the atmosphere from the exposed seed surface. In this case, smaller seeds tended to germinate to a greater extent than large seeds, as the large seeds had a greater exposed surface from which water could be lost.

2.2.2 Effect of soil strength on seed swelling and radicle elongation

Even though soil water potentials may be favourable for seed water uptake, soil particles may exert a counter pressure which may limit seed swelling, and hence restrict uptake of water. Consequently, germination may be delayed due to the soil's mechanical strength (Collis-George and Williams, 1968). This could in part be due also to the radicle's inability to elongate. Stout et al. (1956) noticed a delay in time to 50% emergence with more compacted soils.

2.3 SEED WATER MOVEMENT

2.3.1 Resistance to Movement

Resistance to water movement in the soil has received relatively much more attention than the resistance found in the seed. To a large extent this is justifiable in that soil occupies a much larger volume than seeds under field conditions. Hence soil resistance becomes more important as soil water may have a greater distance to travel. Nevertheless, resistances to water movement within the seed play an important role in the uptake characteristics of a seed.

Shaykewich and Williams (1971a) examined the resistance to water absorption in rapeseed (Brassica napus). Resistance was an inverse function of the water content of the seed. Initially the resistance was very great, but as water content increased, it dropped very quickly. It was suggested that seed hydraulic conductivity is the limiting factor initially even if the soil water potential is at the lower end of the available water range. As the seed imbibed water, however, its hydraulic conductivity increased rapidly, so that the soil's hydraulic conductivity during the latter stages of imbibition became limiting. A wetter seed would have a greater area of flow which would reduce the tortuosity and hence increase the hydraulic conductivity.

Becker and Sallans (1956) demonstrated that at low water content, water moved in wheat seed as thin films of bound water. Since bound water has a higher activation energy than free water, its movement should be temperature-dependent. At greater moisture contents, the microcapillaries in the seed would be saturated, resulting in the presence of free water whose movement is temperature independent. Becker and Sallans suggested that the transition zone between bound and free water occurred near 20% water. Variations in the calculated transition value could result from a lack of equilibrium or a hysteresis effect.

2.3.2 Imbibition phases of germination

Water uptake by living seeds has generally been determined to be triphasic (Bewley and Black, 1978; Takahashi, 1980). The initial phase is quite rapid as there is a greater water potential gradient and strong matric potentials are being exerted by the interior cell walls. Shull (1920) explained the rapid initial hydration by stating that the seed coat is quickly hydrated or suggested that initially for a brief time the seed is in contact with liquid water. During the second phase, uptake rates drop to a more moderate level. It is during this phase that the seeds get activated for germination. Shull subdivided this phase into two phases, with phase 2a having a higher rate than 2b, since levelling off occurs in 2b as the seed approached saturation prior to germination. He noted that the transition between these phases is not smooth but that small shoulders occur between regions. In the final phase, rapid uptake commences again and is due to growth associated with germination. The shape of the curve depends not only on temperature and water supply, but also on the state of dormancy (Takahashi, 1980). Dormant seeds have a longer second phase. Dead seeds lack the final phase entirely as there is no germination.

The first two phases, which encompass the time between seeding and the beginning of germination may be referred to as the lag period.

2.3.3 Affinity to water by various polymers

Since a seed or kernel is not homogeneous, but has both structural and chemical disparities, it is logical that different locations will each exert their particular influence on water flow resistance. The degree of porosity as well as the water holding capacity and hydrophilicity of the various polymers will be influential.

Bushuk (1966) examined the distribution of water in the various components of flour. On a dry weight basis, the proteins and pentosans took up 2.15 and 15.0 times their weight in water respectively, whereas the value for undamaged starch was only 0.44. Even though these values represent only the flour portion and not that of the total seed, and any contribution which structurally intact seeds might exert was not considered, these values given an indication of the water binding of various components in the kernel.

Lee and Stenvert (1973) noticed that different wheat varieties had varying pentosan contents. They suggested that due to the high hydrophilicity of the pentosans, the binding of water limited the water penetration through the seed coat. Similarly, pentosans in the sub-aleurone layer delayed hydration of the more interior regions. The degree of branching of the arabinoxylans found in the bran influenced water penetration, with greater branching inhibiting water movement to a greater degree.

Badenhuizen (1946) examined the swelling characteristics of starch grains. Its structure consists of a series of layers, consisting of many different types of carbohydrates. He concluded that the elasticity of the starch grain is determined by water content, the length of the side chains, and the weakening of lateral cohesive forces. The surface tension of water plays an important role in that it forces water molecules into the starch, widening or stretching the mesh network. At a critical water level, the linkages break due to great stretching. This event is irreversible.

2.3.4 The pericarp, testa, and micropyle

Babbitt (1949) examined water vapour uptake in wheat kernels, some of which had the pericarp removed. He determined that the pericarp had virtually no effect on the uptake curves, suggesting that resistances in the seed rather than in the pericarp limited water uptake. Wellington and Durham (1961), however, suggested that differences in the mechanical properties of the pericarp might be responsible for the differences in germinability between red and white wheats.

When exposed to liquid water, the pericarp is very rapidly hydrated and has a high hydraulic conductivity (Hinton, 1955; Briggs, 1978). Becker (1960) suggested that the rapid hydration was due to capillary forces in the pericarp.

When barley seeds are exposed to liquid water, the surface layers, the husk and pericarp are all hydrated within two hours, whereas in the naked seed, the pericarp is hydrated within 30 seconds (Briggs, 1978).

Moss (1973) noticed a varietal effect on bran structure in wheat. The Australian variety, which had a very open bran structure, had very rapid water entry and easy movement. Krauss (1933) examined the developmental seed anatomy of various grasses and cereals. Associated with maturity were air gaps in the parenchyma cells of the pericarp. These gaps were not present in the unripe kernels.

Similarly, Menge (1979) noticed that the size of the pericarp is reduced after fertilization, a reduction that continues until ripeness. Parenchyma cells found in the inner pericarp disintegrate. The inner epidermis of the pericarp partially disintegrates. There appeared to be a change in the structure of certain cell walls affecting permeability of gases and solutions through the pericarp and testa, which result in increased germinability (Khan, 1977; cited in Menge, 1979).

Mitchell et al. (1980) determined that drying of the pericarp was necessary in making a kernel germinable after anthesis. The pericarp began to lose water about 10 days after anthesis and had lost over half of its water when germinability began to rise at about day 30. Since pericarp weight is relatively small relative to total kernel weight,

total kernel water did not have to go down to any appreciable extent in order for the pericarp to reach the critically low level. Mitchell et al. determined that the pericarp exerted some kind of inhibition on germination until it was either dried, damaged, or removed. It would seem logical that the role of pericarp drying is the irreversible formation of air channels. It is important to remember that Mitchell only considered germination in the study and not water uptake as Babbitt did, and the two factors need not be completely related. Nonetheless, it is reasonable to suggest that the air channels formed as the result of drying would provide a route for rapid water movement. However, seeds not dried and therefore lacking the air channels, might still have an adequate amount of water uptake required for germination.

Evans et al. (1975) suggested that kernel drying induced a hormone sensitivity which would affect the level of dormancy. It is possible that drying alters inhibitor structure making them inactive, or in some other way affects the inhibitor independent of the pericarp structure. However, the air channels in the pericarp might redirect the water causing it to move parallel with the seed surface before entering the seed. This could affect the location of hormones in the pericarp, and therefore the seed's awareness of these hormones, thereby also affecting the seed's ability to germinate.

Belderok (1976a) stated that dormancy is often associated with the coat layers of the wheat kernel, but the low water uptake associated with mechanically tough seeds was not the limiting or controlling factor. Belderok (1976b) examined the changes in the seed coat which occurred during dormancy and after ripening. Sprouting resistant varieties of wheat tended to have a thicker testa, which was fairly homogeneous in structure and remained structurally stable during after-ripening. Resistant varieties also had a higher sulfur content in the testa, a value which declined during after-ripening. Susceptible varieties had a thinner testa which became granular upon after-ripening.

Hinton (1955) reported that in wheat, the testa offers the greatest resistance to water movement. He failed to find a good correlation between kernel characteristics such as colour, size, thickness of skin, or exposure to adverse environmental conditions and the water permeability through the testa.

Brown (1909) studying barley seeds determined that the membranes in the seed coat had semi-permeable characteristics. Different solutes ranged from non-diffusable to diffusable. The diffusion properties were associated with the degree of ionization, surface tension, and viscosity. Inconsistancies between these characteristics and diffusion were explained by interactions occurring between the solvent and solute affecting the diffusion. Brown and Worley (1912)

determined that increased temperature increased the uptake rate. Brown and Tinker (1916) determined that the selective permeability was so strong, that seeds took up phenol and aniline to higher concentrations than found in the ambient solution.

Water uptake in the kernel appears to be preferentially located at the micropylar or embryo region (Brown, 1907; Collins, 1918; Blacklow, 1972; Stenvert and Kingswood, 1976). The outer cuticle found covering the rest of the kernel does not cover the micropylar region (Krauss, 1933). Stenvert and Kingswood (1976) demonstrated that the embryo contained much more water than the endosperm in wheat after short periods of damping. Briggs (1978) carried this further, saying that the embryo had a higher final water content, and was also the first to lose water upon desiccation. Since the embryo and endosperm both have fairly similar energies of activation ranging from 3.2 to 3.4 Kcal/g. mole/ degree C. (Briggs, 1978), it would be safe to state that the easy water transfer through the micropylar region is responsible for these differences.

Given the fact that the testa is fairly impermeable to water, the air channels in the pericarp might well serve as a transport pathway toward the micropylar uptake site. Inhibitors and/or promotors found in the pericarp could therefore rapidly be transported directly to the embryo and determine the seed's germinability.

2.3.5 The embryo and endosperm

The embryo exerts a significant effect on the breakdown of endosperm. As early as last century, Brown and Morris (1890) determined that endosperm degradation was reduced if the embryo was excised. Using intact seeds, Brown and Morris also noticed that endosperm degradation began near the scutellum and proceeded into the endosperm parallel to the scutellum.

Endosperm breakdown advanced faster near the aleurone layer as disintegration progressed away from the scutellum, suggesting that the aleurone also is involved (Briggs, 1972). It is generally accepted that gibberellic acid (GA) is released from the embryo through the scutellum and diffuses to the aleurone layer. Here it stimulates hydrolytic enzyme production which in turn are released into the endosperm (Bewley and Black, 1978). The significance of GA was demonstrated by Black (1969; cited in Bewley and Black, 1978); CCC, a substance which blocks the production of GA, was successfully used to prevent germination.

Using electron microscopy Stenvert and Kingswood (1977) determined that endosperm structure significantly influenced hydration. The more ordered the structure, the slower the water movement. High protein also tended to slow movement. The more ordered structures which are normally referred to as being vitrious or steely have a glassy or flinty appearance whereas the less organized mealy endosperm

appear floury or opaque (Briggs, 1978). Hinton (1955) looking at both soft and hard wheats, concluded that a mealy endosperm was about twice as permeable to water as a vitrious one. Mealy seeds had greater capillary forces enhancing water movement. Briggs (1978) states that mealy grains have less physical cohesion to resist swelling. Freezing and thawing or wetting and drying tended to make a grain more mealy due to fracturing of the endosperm caused by the very strong forces the kernel was exposed to. Since mealy grains take up water more rapidly and have a lower resistance to swelling, they normally germinate more rapidly.

Milner and Shellenberger (1953) noticed a decline in wheat kernel density upon weathering. Wetting and drying cycles induced the formation of internal fissures. Immature kernels did not fissure upon initial drying, but fissured only when dried a second time after being rewetted. This would suggest a structural endosperm change is associated with maturation.

Dorsal endosperm cells appear to be smaller and more elongate than those in the mid-cheek region in wheat. The average density is lower in the dorsal region than in the cheek centers (Campbell and Jones, 1955).

Shelef and Mohsenin (1966) examined the equilibrium moisture contents of corn kernels at various humidities. When the external relative humidity levels were below 88%, the endosperm had a somewhat higher water content than the

embryo at equilibrium. At higher relative humidities, the opposite was true. The 88% humidity corresponded with approximately 20% seed water content. This moisture-content water affinity interaction is similar to that observed by Bushuk and Winkler (1957) when they studied gluten and starch. This shift in the strength of the affinity to water could result in water migration from one region of a seed to another, and again temperature would be influential.

Jones and Campbell (1953) and Campbell and Jones (1955) examined the density of endosperm in intact wheat kernels and semolina which are coarse milling fractions. In intact kernels, an abrupt change occurred at about 20% moisture. If a dry seed was moistened up to 20% moisture, there was only a small decrease in endosperm density, whereas further moistening resulted in a substantial density reductions. This drop in density past 20% moisture was the result of increased swelling. The semolina did not show this response but resulted in a gradual drop in density with increased water throughout the entire moisture range including moisture values below 20%. Shearing forces exerted in the mill had destroyed whatever structural component is involved in maintaining the swelling resistance at less than 20% moisture.

Shelef and Mohsenin (1968) examined the stress-strain interactions in corn endosperm. At moisture contents below 20%, deformations caused by increased stress were very

small. However, the seed was inelastic and any deformations were permanent. At water contents above 20%, there were very large changes in the residual deformations with a low stress. These deformations were plastic. As stress increased, great increases in deformation occurred but these were reversible or elastic. However, at some critical stress level called the yield point, the whole structure deteriorated. At greater water contents, the yield point occurred at lower stress but higher strain values. Greater elasticity was also associated with higher moisture contents.

At about 20% moisture, the seed appears to undergo structural modifications from an elastic or rigid structure with a limited water holding capacity to a plastic structure which can swell quite freely with the uptake of additional water.

2.3.6 Water entry at the brush region

Mechanical damage may affect the seed's integrity, altering its imbibition and germination responses (Campbell, 1958). Campbell noticed rapid hydration of the dorsal regions of the endosperm in the Manitoba but not in the British wheat samples be observed. Damage at the brush region would allow easy entry to water beneath the pericarp by capillary action. Campbell exposed mechanically damaged brush ends to dye, and noticed that the dye entered under the per-

icarp and rapidly moved along the dorsal surface toward the embryo. It is reasonable to assume that brush damage commonly occurs during machine harvest.

Brush characteristics such as the length and number of hairs, and the area on the surface occupied vary depending on the variety. Hexaploid wheats tend to have a dense mass of long hairs. Durums have fewer shorter hairs. In many wheat varieties, the brush is separated from the dorsal surface by a collar, which essentially consists of a fold in the pericarp. Bradbury et al. (1956) determined that air generally occupies the space in the collar region. It is possible that the damage to the brush and/or collar allows water to enter the air gap in the collar and from there to enter beneath the pericarp.

2.4 THE EFFECTS OF TEMPERATURE AND WATER POTENTIAL ON GERMINATION TIME

Dubetz, et al. (1962), demonstrated that warmer temperatures accelerated germination in both spring and winter wheats between 6 and 24 C. Both temperature and water potential affect the duration of the lag period. Blackshaw et al. (1981), using polyethylene glycol solutions to control water potential, determined that lower water potential increased the lag period in wheat seeds, but had no noticeable effect on the germination rate once germination began. Similarly, colder temperatures increased the lag time but had no effect on the slope of germination (Hallem, 1981;

Blackshaw et al., 1981; Khan, 1977). What is more surprising, however, is that the slope for emergence was unaffected by lower temperatures; again the only thing affected was the lag period. This is unexpected, as one would imagine the growth Q10 of 2 to 3 to delay root and shoot growth, thereby slowing the rate of emergence. During the lag period, the seed must undergo some sort of physiological modification, thereby making it more adaptable for the temperature conditions it is in. Blackshaw et al. (1981) also examined the temperature response in green foxtail (Setaria viridis). This C-4 species behaved quite differently than the wheat. At warmer temperatures decreases in water potential increased the lag period but did not affect the germination slope. However, at cooler temperatures, the slope of germination fell with a decrease in water potential. This would indicate that green foxtail is not as well adapted to cooler temperatures as wheat.

2.5 POST-HARVEST DORMANCY

Seeds contain substances which both promote and inhibit germination. Levels of the germination inhibitor abscisic acid (ABA) tend to drop as the seed reaches maturity while simultaneously gibberellic acid (GA) responsiveness tends to go up (Heydecker, 1972). Possibly in sprouting resistant varieties, these reactions might be delayed.

Drying of the grain tends to make it more germinable at maturity (Nicholls, 1979; Mitchell, et al., 1980). There is no conclusive evidence that the drying is responsible for the reduced ABA levels. The rate of drying of a detached kernel influences its subsequent responsiveness to GA, slow drying giving the highest response (Nicholls, 1979; King and Gale, 1980). Nicholls (1980) reported that the temperature and the rate of drying were influential. Allowing heads to mature between 4 and 30 C, he determined that at temperatures below 16 C there was a gradual increase to GA responsiveness as temperature increased, when the GA was applied to the non-embryo end of the seed. At temperatures above 20 C, applied GA did not have all that much of an effect, as amylase was produced with or without the GA. In terms of the inhibitor - promoter battle, grains matured at low temperatures could still contain some ABA whereas the warm matured seeds might have lost all ABA, and produced its own GA. Nicholls also conducted an experiment in which non-embryo seed halves of both warm and cool temperature matured seeds were placed end to end with only some dialysis membrane separating the two. The membrane was used to prevent amylase movement, but still allowed both GA and ABA transfer. The results demonstrated that amylase was only present in the warm seed half, suggesting that neither GA or ABA was present or produced, at least not in measureable quantities. It is important to realize that the participation of the em-

bryo was not considered in this experiment, and may well be a source of both promotors and inhibitors.

Other evidence also suggests that a kernel's germinability and dormancy are influenced by environmental conditions, especially around maturity. Stoy and Sundin (1976) observed a number of unharvested wheat cultivars for three months after maturity, and regularly observed germinability, moisture content, and amylase production in response to added GA. Only results of four cultivars of a total of fourteen examined in the original experiment were reported in the paper. All cultivars had a common sharp decrease in moisture content at maturity. Subsequently, due to environmental conditions, moisture oscillated between 15 and 30%. In three of four cultivars, GA responsiveness and germinability oscillated in synchrony with the moisture content of the kernels after the initial drying. In the fourth cultivar, Kleiber, oscillations between moisture content and GA responsiveness and germinability were much smaller. In all of these results, the onset of germinability was associated with the initial drying. However, in one cultivar, Snabbe, GA responsiveness was delayed by about a month. Moreover, in the cultivar Jan, GA responsiveness remained relatively low, despite the fact that germinability rose to very high levels. This would indicated that even though GA responsiveness and germinability oscillate in syncrony with moisture content, they are not completely linked to each other.

Examining the germinability of excised embryos, Stoy and Sundin also noticed that interactions between GA and ABA or catechin tannins also oscillated with moisture content. This is fascinating, given that the excised embryos were exposed to ample water for the several day duration of the experiment, and still responded in synchrony with the water content of the whole kernel prior to being excised.

2.6 WATER SENSITIVITY AND COUMARIN

When a seed displays water-sensitivity, its germinability is similar to normal seeds except under very wet conditions. Exposure to liquid water significantly depresses germination. If semi-dormant barley is set to germinate in petri plates with filter paper and volumes of water greater than 4 ml., germination is markedly delayed (Pollock, 1962; Jansson 1959; Briggs, 1978). Essery et al. (1955) determined that the effects of water-sensitivity could be overcome by intermittantly giving the seeds air or oxygen.

Jansson (1959) determined that the addition of coumarin to non-water-sensitive seeds made them behave like water-sensitive seeds. Pollock et al. (1955); cited in Jansson 1959) suggested that the main cause of water sensitivity was the pericarp which prevented adequate oxygen penetration. Jansson (1959) suggested that the lack of oxygen prevented a necessary oxidation reaction - a reaction which de-

stroyed or deactivated an inhibitor. By peeling the pericarp off of grains, water sensitive grains lost their sensitivity (Jansson 1959) and eliminated the inhibitory effects of coumarin treatment (Pollock et al, 1955 cited in Jansson, 1959). Coumarin could therefore act as a replacement inhibitor of the pericarp in non-sensitive kernels causing them to become sensitive.

Water sensitivity and the coumarin responses tie in well with the earlier stated idea suggesting that air channels in the pericarp caused as a consequence of drying, determine the kernel's germinability. It appears that water sensitive seeds may not have dried sufficiently to induce the formation of these air gaps.

The pattern of response to coumarin appears to be similar to that of a developing grain. It is necessary that the embryo be prevented from germinating during development, given that ample water is available. However, this inhibitory action should not be so strong as to restrict germination once the seed is in the soil. Under normal conditions, the seed would probably have dried to a certain extent and water availability in the soil would usually be more limiting.

2.7 SEED PRESSURE

The initial water potential of air dry wheat seeds is low, often lower than -1000 bars (Shaykewich, 1973). Countering this negative potential is a positive swelling pressure of the same value. As the water potential increases upon imbibition, the swelling pressure decreases. At around 20% moisture, the water potential and the swelling pressure equalled close to -400 and 400 bars respectively. At 50% moisture, these values had reached -30 and 30 bars already.

The effects of pressure during seed imbibition have not been adequately studied. Waggoner and Parlange (1976) studied water uptake in pea seeds and noticed distinct boundaries between wet and dry regions during imbibition. Since water has a stronger affinity for pentosans and proteins than to starch (Bushuk, 1966) and since water has sites of preferential entry into the seed, there are often localized areas of high water content. Due to the high water content in these regions, intense swelling pressures are produced. These high positive pressures will counter-balance the negative water potential and the higher water content will increase the vapour pressure, resulting in a delay or even a reversal of hydration. With time, the structure may give way yielding to the pressure.

Pressure has been documented to strongly influence some of the deep-dwelling sea organisms. Hochachka and

Somero (1973) demonstrated how enzymes of deep sea organisms were only activated if pressure was in excess of 100 bars, whereas surface habitants expressed the reverse behaviour. It is suspected that changes in protein configuration due to pressure were responsible for this reversible behaviour, affecting the enzyme affinity for substrate and activator molecules. At 20% moisture, wheat had a swelling pressure of close to 400 bars, four times that required to activate the enzymes in the deep sea dweller. Yoshida et al. (1979), using barley noticed that only 1.5 bars of hydrostatic pressure was required to affect barley germination. High pressures can result in conformational changes in proteins and other polymers. As well as affecting enzymes, changes in hydrophobicity and hydrophylicity of subunits could affect water relations.

2.8 VAPOUR PHASE UPTAKE

One of the major problems associated with rapid water uptake by seeds is that the water in the seed is not in equilibrium. Generally, the area of the seed closest to the water source has a higher water content than the rest of the seed. Studies involving seed properties at various water contents may be deceiving in that the calculated or given water content will be the average water content. Slow uptake gives the water a chance to equilibrate, so that the water potential is more uniform throughout the seed.

A much slower uptake method using water vapour was examined by Babbitt (1949) using wheat seeds. By examining both the wetting and drying curves he determined a hysteresis effect. Hunter and Dexter (1950) using sugar beet seeds at various humidities at room temperature, determined that higher humidities increase the final equilibrium water content. Owen's (1952) classic vapour water uptake and germination studies confirmed earlier findings of higher relative humidities causing a more rapid uptake. Owen also examined whole and embryo-excised seeds. Both had the first two phases of the triphasic water uptake pattern, however, as expected, the embryo-excised seeds lacked the final phase. Owen also varied the distance between the liquid water and the seeds, but there was no appreciable difference, and therefore suggested that the seed offered a greater resistance than that caused by the distance the vapour had to travel.

2.9 TEMPERATURE AND DORMANCY

The seed ecology literature provides some insight as to how dormancy is regulated by temperature. Thompson (1970) demonstrated how seeds displayed dormancy only where they were exposed to temperatures above or below some definite range. Loss of dormancy was associated with an increased range of temperatures in which the seeds would germinate through a shift in one or both boundaries.

Similarly, Vegis (1964) concluded that the growth potential of dormant organs was closely related to the temperature. Generally, non-dormant organs could grow over a much wider temperature range than their dormant counterparts. As an organ entered dormancy, the temperature range narrowed, but widened again after dormancy. Various species responded differently having either low, high, or low and high temperature boundaries. Vegis pointed out that even if a dormant seed was in the restricted temperature range required for germination, such an occurance could be overruled by an inhibitor. MacKey (1976) studying wheat, oats, and barley only found an upper boundary. Temperatures above a critical level expressed dormancy in the dormant seeds whereas non-dormant seeds germinated across the whole temperature range. Andrews and Burrows (1972) using dormoat, a cross between Avena fatua and Avena sativa, determined that at 20 C total germination was low, but with colder temperatures, germination increased with 7 C being optimal. Smith and Roberts (1977) examined the effects of temperature on dormant barley. They determined that the time to 50% germination at temperatures below 18 C was similar to values obtained using non-dormant barley as germination was rapid. However, at temperatures of 20 C or warmer, the time to 50% stretched to about 700 hours. A very sharp temperature boundary occurred between 18 C and 20 C. Gosling et al. (1981) demonstrated that fresh prematurely harvested wheat seeds germinated best

at temperatures below 10 C and were quite dormant at warm temperatures. As seeds matured, the range in temperature in which germination occurred widened, and the optimal germination temperature on the germination curve varied depending on the time after anthesis. At times the response was quite gradual or smooth, but at 50 days after anthesis a sharp temperature effect was observed between 18 C and 20 C just as had been the case in the work of Roberts and Smith. At 63 days after anthesis, the dormancy appeared to have been lost as the wheat germinated rapidly across the entire temperature range.

Temperature effects such as these are often explained in terms of sharp effects temperatures have on membranes. However, it can also be argued that the phase properties of the structural polymers found in the seed are involved.

Both temperature and seed structure affect water uptake. Campbell and Jones (1957) found that the rate of water penetration varied throughout the endosperm. The dorsal region wetted a lot sooner than the cheek centers on the ventral side. At room temperature, it took about 40 hours before moisture equilibrium occurred. Increased temperatures greatly increased the rate of water movement to the cheek center region with a Q10 of about 2.4. The maximum temperature which yielded a response was 43.5 C. A brief 30-minute treatment at 43.5 C greatly decreased time to

equilibrium when the seed was returned to 20 C. This would suggest that at high temperatures an irreversible event occurs which enhanced the rate of movement. High temperatures more than likely get rid of or melt some structure which impedes the movement of water. This information is in keeping with the work of Bushuk and Winkler (1957) where it is noted that a shift in temperature resulted in a redistribution of water between the polymers contained in the seed.

Khan (1977) reported on a number of studies in which seeds of warm temperature crops, if brought slowly to 18% moisture under warm temperature could subsequently germinate vigorously at temperatures below 10 C, whereas seeds not conditioned in this manner would be damaged or killed if subjected to such low germinating temperatures. Cal and Obendorf (1972) studied the effects of initial water content in corn (Zea mays) kernels on germination at different temperatures. When kernels containing low amounts of water were exposed to 5 C germinating conditions, delayed and quite abnormal germination occurred. On the other hand, if the seeds were brought to 16% moisture prior to being exposed to the cold germinating conditions, they were protected from the chilling injury and germination was more similar to that of warmer temperatures.

Lower temperatures normally result in more water being bound rather than free. As well, the rate of water movement tends to be retarded at low temperatures. These

combined factors would tend to result in very non-uniform water distribution throughout the seed. Consequently, intense swelling pressures would occur in the wet regions. The dry regions, still having an air dry water content, would not be plastic but rigid. The resulting stress caused by the uneven pressure and rigidity could cause fracturing of portions of the seed resulting in damage. Seeds preconditioned to a higher moisture level would be more plastic, allowing them to withstand and adapt to greater swelling pressures associated with cold conditions.

Tanaka (1980) demonstrated how temperature had a critical effect on the swelling characteristics of acrylamide gels. At temperatures below 20 C, the gel was collapsed whereas at 20 C or warmer, it was in the fully-swollen state. Using small 0.5 cm. gel pieces, equivalent to the size of many seeds, Tanaka demonstrated that thermal equilibrium occurred very rapidly, within seconds, whereas several days or weeks were required for the pieces to become fully hydrated.

These results quite vividly demonstrate the effects of temperature on structure. Such structural modifications also explain the sharp temperature effects on germination.

Bushuk and Winkler (1957) studied the absorption characteristics of water vapour on wheat flour, starch, and gluten. At water contents above 20%, the activation energies for water movement were close to 10.7 Kcal/mole which

is the heat of vapourization of liquid water. However, as the water content decreased below this level, the binding energy increased, resulting in a greater value. Simple sorption theory would predict a smooth curve relationship between moisture content and the binding energy. In Bushuk and Winkler's case this, however, was not evident, as peaks or bumps occurred on the curve at different locations depending on the fraction involved. The binding energies of the different polymers also varied at a given moisture level. In fact, the curves for starch and gluten crossed over in the moisture range studied. Conformational changes in the absorbing polymers alter their affinity for water and explain the presence of the peaks on the curve (Adamson, 1967). Changes in temperature would result in a change in vapour pressure, and would result in movement away from the fraction having the lower change in heat of vapourization. As a consequence, during drying conditions at moisture levels below 20% where conformational changes do occur, small changes in temperature would result in differential rates of water loss from the different polymers.

Studies involving intact wheat seeds demonstrate that the relationship between vapour pressure and moisture content is not represented by a smooth curve. Collis-George and Melville (1978) came up with a smooth curve, but further analysis of their data reveals that the Q10 for moisture varied anywhere from 1.0, which is temperature insensitive,

to almost 2.0. Using their data, the Q5 values were calculated on the range of temperatures and water potentials. The most striking result occurred at about -400 bars. At this water potential, a very low Q5 trough ran through all temperatures. This is interesting in that -400 bars closely corresponds to 20% water content in wheat. The 20% value noted by Jones and Campbell (1955) was the transition value of the seed's swelling properties from rigid to plastic. The Q5 values at other water potentials were generally considerably greater, especially at wetter conditions. A small trough occurred at about -1600 bars, the Q5 being especially low between 25 and 30 C at that water potential. Since this plot is not smooth, but has troughs and peaks, it is apparent that temperature interacts with the structural character of the seed, which is determined by the water content, in influencing further water uptake.

When closely looking at some of the data of vapour phase uptake experiments, it becomes evident that during the uptake phase when rates had levelled off, there were instances when the seed actually lost some water (Owen, 1952). These losses likely were due to small temperature effects which altered the polymer characteristics and possibly affected the swelling pressures in the seed.

When a dry seed is exposed to water, heat is given off when the water and starch bind. The amount of heat given off can be great enough to significantly increase the

temperature of the seeds (Collis-George and Melville, 1978). This increase in temperature could slow down further vapour uptake.

Blacklow (1972) examined the temperature moisture effects on germination in corn. He determined that the temperature optimum occurred at about 30 C with depressed rates occurring at lower temperatures. Moisture content at the time of radicle penetration was affected by temperature. Colder conditions resulted in a much greater water content at the time of germination. Perhaps the reason for reduced rates of corn germination at colder temperatures is due to a greater moisture requirement at these temperatures. Colder temperatures may inhibit or alter the structural modifications which occur at warm temperatures, and this may be part of the reason for a higher water requirement.

Chapter III

MATERIALS AND METHODS - GENERAL INFORMATION

3.1 BIOLOGICAL MATERIALS

Seeds used in most cases were Triticum aestivum Neepawa, and Triticum aestivum Norstar. The hard red spring wheat Neepawa was a product of the uniform testing trials of Winnipeg in 1979. Protein content using the Kjeldahl method was determined to be 17.9% on an oven dry basis. The Norstar winter wheat was produced at The University of Manitoba as part of a yield trial in the 1980 growing season and had an oven dry protein content of 12.9%. The moisture content of both air dry wheats was determined to be near 11% on a dry weight basis. Viability of the seeds was determined to be very close to 100%. After testing numerous 50-seed subsamples of both wheats, final germination after 14 days under conditions of 10 ml. water per 65 g. fine silica sand at 15 C ranged from 98 to 100%. Similar tests under very wet conditions showed no water sensitivity. A 100% viability was assumed.

Two small samples of dormant Neepawa wheat were obtained for use in one section of experiment IV. They were produced at The University of Manitoba in the 1980 growing

season, and harvested before the kernels were mature. Upon harvest, they were immediately frozen in air tight containers to retain the post-harvest dormancy until use. (Noll and Czarnecki, 1980)

In order to compare Neepawa with some other varieties, T. aestivum Columbus, T. aestivum Glenlea, and T. durum Leeds were included in the dye experiment. These seeds were produced at The University of Manitoba in the 1980 growing season.

3.2 SIZE GRADING OF SEEDS

3.2.1 Seed Sieving

In order to reduce the size variability of seeds within a seed lot, they were graded into subsamples. With both wheat varieties, the initial step consisted of passing the seeds through a series of screens. The openings in the screens were long, narrow rectangles. The length of the slots was a constant 20 mm. The width of the slot varied in size, being either 2.8, 2.4, or 2.0 mm. depending on the screen. These rectangular slots appeared to give superior seed separation when compared to similar screens with round holes, due to the non-spherical shape of wheat kernels. Seeds wider than the 2.8 mm. slots were classified as large. Seeds narrower than 2.8 mm. but wider than 2.4 mm. were classified medium. Similarly, seeds between 2.0 and 2.4 mm. were classified as small. Any seeds smaller than 2.0 mm.

were discarded due to very small numbers and questionable quality and vigour. The Neepawa seed lot had approximately 40% of the total seed volume in the large, 40% in the medium, and 20% in the small fraction. The Norstar had 35% in the large, 40% in the medium, and 25% in the small fraction. It is important to distinguish these values from seed number values. Even though the small size fraction occupied a smaller amount of total volume, the actual number of small seeds may have been similar to the number of other seeds in another fraction.

3.2.2 Air Classification

Further subdivision of these fractions was possible by using an air column separating apparatus. The unit, which more commonly is used to separate chaff from seeds consists of a long vertical plexiglass column 11 cm. in diameter and having a height of 80 cm. Seeds were placed at the bottom of this column. An adjustable air stream entered at the bottom of the column. Lighter material tended to move upward whereas heavier material tended to stay near the bottom. Diagonal traps near the top of the column prevented material reaching that height from falling down again. In separating the wheat, a fairly rapid airflow was necessary, as wheat seeds are fairly dense. After placing seeds in the column, air flow was gradually increased until the amount of seeds trapped near the top was equal to the amount remaining

below. The top fraction was classified as the light fraction while the bottom fraction was called the dense fraction. The light and dense terminology may not be entirely accurate, as no actual density values were determined. Size variability within the screened fractions could allow smaller seeds to reach the top of the column with greater ease as such seeds would have a greater surface to volume ratio, and hence a greater surface to mass ratio. However, since the size range within a fraction was small, seed density likely was the major cause. A Strong-Scott barley pearler was used in demonstrating that the medium dense seed was harder than the medium light seed. The pearling resistance value, which represents the material remaining (pearls) in grams from 20 gm. samples after 20 seconds of pearling gave values of 9.2 and 10.1 grams for the light and dense fractions, respectively. Pearling values are only relative since there are considerable differences between pearling machines and since different researchers use varying sample weights and times in their studies.

3.3 GERMINATION MEDIUM

Acid washed very fine silica sand (Fisher Scientific) of a narrow range of particle sizes (85 - 125 mesh) was used as a medium to germinate seeds.

In most experiments, 65 g. of the sand was mixed with 3 to 15 ml. water. Although this represented a wide

range in gravimetric water content (0.046 to 0.231 gm. water/gm. sand), the range in water potential was quite small. Given the relatively large particle size of the sand, slight decreases in water potential resulted in large decreases in water content. Tension plates were used in determining the water potential - water content relationship from 0 to 100 cm. (-0.1 bar). (See Appendix, Figure 43.) This small water potential range encompassed the whole range of studied water contents. Therefore the effect of hydraulic conductivity played a greater role on water availability than water potential.

Chapter IV

EXPERIMENT I - THE EFFECT OF SEED PLACEMENT ON A MOIST SAND SURFACE USING SIX SEED SIZES

4.1 INTRODUCTION

It was decided that many water uptake studies in this research project were to be conducted by placing wheat seeds on top of a moist sand surface. The easiest way to go about this would be to dump seeds on top of the sand, making sure they were fairly evenly distributed. This procedure would result in seeds lying crease-down, sideways, or crease-up on the sand surface. Since orientation of the seed could affect the uptake and germination characteristics, an experiment was designed in which the hours to 50% germination of randomly dropped seeds was compared to seeds which all had been positioned crease-down. It was decided that if there was no difference between the two, seeds in subsequent experiments would be in the random drop position. Water uptake in crease-down seeds might be enhanced due to greater seed-sand contact areas from the two cheeks. On the other hand, Campbell and Jones (1957) demonstrated that the endosperm in the cheek region was slower to wet than that of the dorsal region.

4.2 MATERIALS AND METHODS

4.2.1 Materials and Methods

A completely randomized factorial experiment involving two different seed placements and six different seed sizes was designed.

Round containers (manufactured by Lab-Tek), 8 cm. in diameter and 6 cm. high, were used to germinate the seeds in. Sixty-five grams of fine silica sand was placed into the containers. Ten ml. water was added to each container and thoroughly mixed with the sand. A one kg. weight dropped from a uniform 10 cm. height was used to pack the sand, to create a smooth surface and uniform bulk density. Fifty seeds were placed evenly on the sand surface in each container. The containers were quickly sealed with air-tight lids and placed into a 15 C germination cabinet.

The seeds were placed either randomly on the surface (crease-down, sideways, or crease-up) or crease-down. The six size fractions consisted of both size graded and mixed fractions. The uniformity in weight of the 50 seed samples within a given fraction was high, usually well within 0.04 gm. of the average weight of that fraction. This was equally true in the size graded as well as in the mixed fractions where more variability might be expected. The seed fractions in ascending weight (50 seeds) were small, overall mix, medium light, medium mix, medium dense, large. Their mean weights are included in Figure 1.

Each of the 12 placement-size combinations had six replicates. The containers were inspected regularly for germination - approximately two or three times daily after the first day. Seeds which had germinated were removed at each inspection. Germination was said to have occurred once the radicle had pierced the seed coat and become visible.

The hours to 50% germination values were determined using linear regression on the germination percentages surrounding 50%.

4.3 RESULTS AND DISCUSSIONS

4.3.1 Results and Discussions

The effects of seed fraction (size/weight) and placement are shown in Fig. 1 and Appendix Table 7. Strong fraction effects were evident and ranged from about 45 to 58 hours in the small and large fractions respectively. Seed placement did not exhibit nearly the same effect and only showed significance at $p=0.05$. Crease-down seeds reached 50% germination about 1.5 hours before the randomly scattered seeds. No interaction was evident.

Heavier seeds resulted in increased time to 50% germination. Seed weight is the consequence of size and density. Since the fractions in most cases were the result of screening, size was the primary factor in determining which fraction a given seed was destined to end up in. Obviously larger seeds required more water uptake in order to reach a

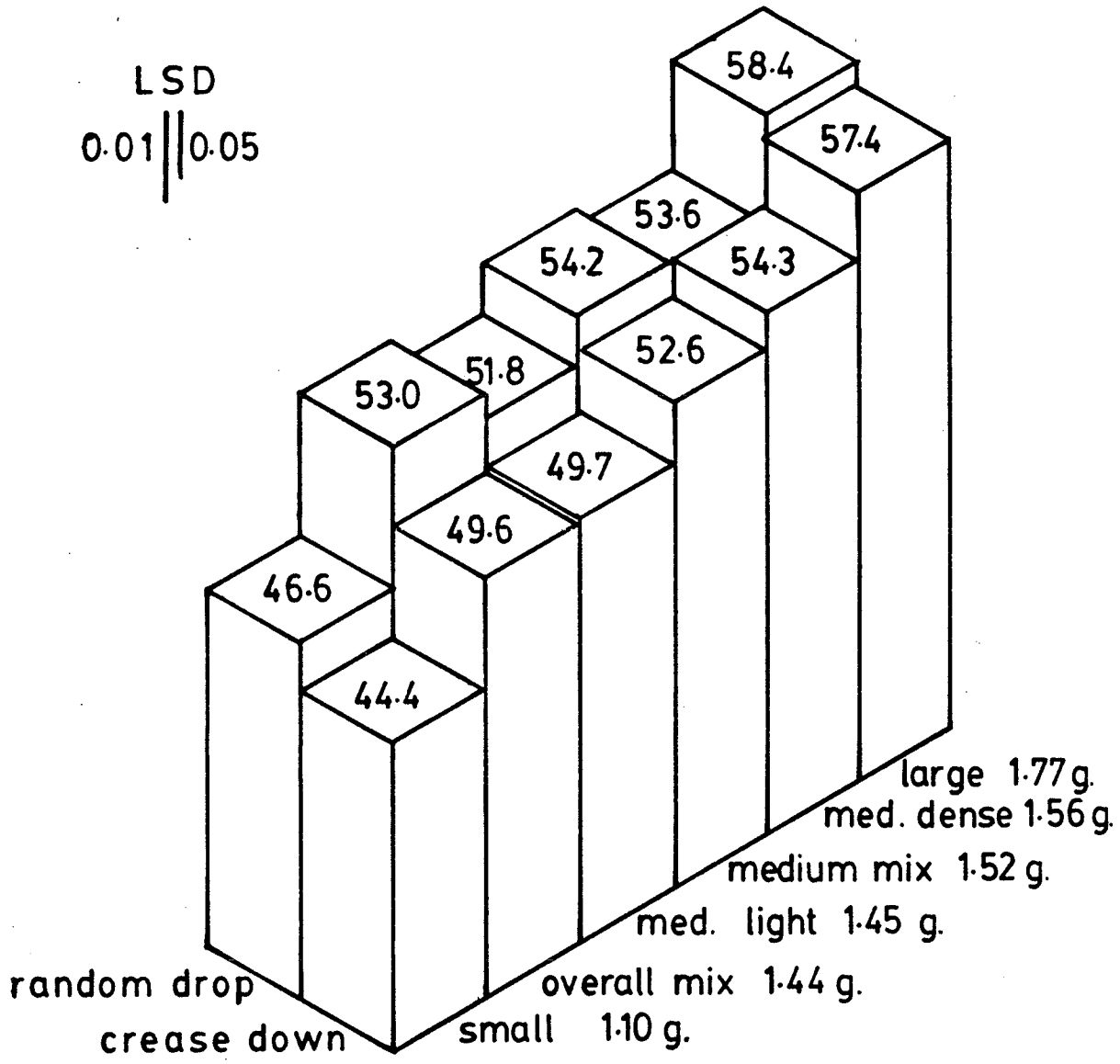


Fig. 1. Mean hours to 50% germination of two seed placements and six seed fractions of Neepawa wheat (with mean 50 seed fraction weights). $L.S.D._{0.05} = 3.14$. Base value = 40 hours.

given water percentage and hence more time. This is in agreement with the results of Hadas (1977) and Muchena and Grogan (1977).

The medium sized dense seeds took longer to germinate than the medium light seeds. Density differences could result from compositional and structural dissimilarities, both of which could affect water movement within the seed (Campbell, 1958; Stenvert and Kingswood, 1976) and hence germination.

Contrary to expectations, the variation between replicates in time to 50% germination in the non-graded mixed fractions (having the whole range of seed sizes) was no greater than that of the size-fractioned seed (data not shown). This could be explained in terms of the mixed fractions being well mixed; that is, all 12 replicates in the mixed samples had similar proportions of the different seed sizes, causing them to reach 50% germination at similar times.

The slightly more rapid crease-down germination values could be a consequence of greater contact area with the sand. However, since the crease-down seeds had to be individually placed into the containers, whereas the random seeds were dumped more or less evenly into the container, it is probably that the crease-down seeds were more evenly distributed on the sand surface. This would result in lower water competition between neighbouring seeds. Experiment

III demonstrated a strong effect of density on hours to 50% germination. Given that the difference between the two placements was not that great (Figure 1), subsequent experiments used the random drop procedure, making sure the seeds were fairly evenly distributed.

Chapter V

EXPERIMENT II - GERMINATION RATES OVER A RANGE OF SAND WATER LEVELS

5.1 INTRODUCTION

Preliminary experiments suggested that germination time was not linearly related to sand water contents, and that possible peaks of rapid germination occurred at certain sand water levels. A fairly wide range of gravimeteric water contents (3 to 15 ml. water in 65 gm. sand) was examined, although this represented a water potential range from only -0.1 to 0 bars. Time to 50% germination was determined across this range for both control and coumarin treated Neepawa seeds.

5.2 MATERIALS AND METHODS

5.2.1 Part A

Water ranging from 3 to 15 ml. with 1 ml. intervals was added to 65 g. fine silica sand, and was prepared as in Experiment I. Hydraulic conductivity was not directly measured, but because of large particle size relative to, for example, clays, it would drop sharply with reductions in water content (Brady, 1974).

Fifty Neepawa seeds of either large or medium size were dropped randomly on the sand surface, and distributed evenly. The containers were immediately sealed to prevent vapour loss, and were placed into a 15 C germination cabinet. The experiment therefore, was a 2 x 12 completely randomized factorial, as there were two seed sizes and twelve water levels. The number of replicates for each of the 24 treatments ranged from 4 to 8. The reason for unequal replicate number was that the experiment began with 2 ml. intervals between the successive water treatments. The harmonic mean for replicates was calculated to be 4.9 and was used in calculating the standard deviation.

Germination counts and the hours to 50% germination calculations were conducted as in Experiment 1.

5.2.2 Part B

Medium-sized Neepawa seeds were treated for one hour in an acetone solution containing 100 mg. coumarin per 25 ml. acetone. Seeds were thoroughly dried with a rapidly moving air current for at least 24 hours before being set to germinate. Two replicate containers of 50 seeds were set up for seven different water levels - 4, 6, 8, 10, 12, 14, and 15 mls. per 65 g. silica sand. Acetone control seeds were also set up.

5.3 RESULTS AND DISCUSSION

5.3.1 Part A

The hours to 50% germination were affected strongly by both water and seed size (Appendix, Table 8). The individual treatment means are shown in Figure 2. The effect of water was not that pronounced between treatments except in one case. Containers having 15 ml. germinated over 20 hours sooner than their drier counterparts. This sharp drop in hours can be attributed to the fact that the 15 ml. treatments had a thin film of liquid water on top of the sand surface, whereas all the drier treatments had their water closely associated with the sand particles. The 15 ml. treatment was essentially similar to the more usual petri-dish filter paper experiments, in which external hydraulic conductivity is not limiting, and water potential is zero.

Differences between the water treatments ranging from 3 to 14 ml. were not large. There tended to be a delay at about 5 ml. and an acceleration at 9 or 10 ml. in hours to 50% germination. Within a given seed size, there were few significant differences, especially at $p=0.01$. More differences were evident in the larger seed size. Using linear regression, the slopes calculated on the mean hours to 50% germination for water treatments from 3 to 14 ml. were -0.133 and -0.137 hours per additional ml. water for large and medium sized seeds respectively. This would indicate that the mean hours to 50% germination decreased

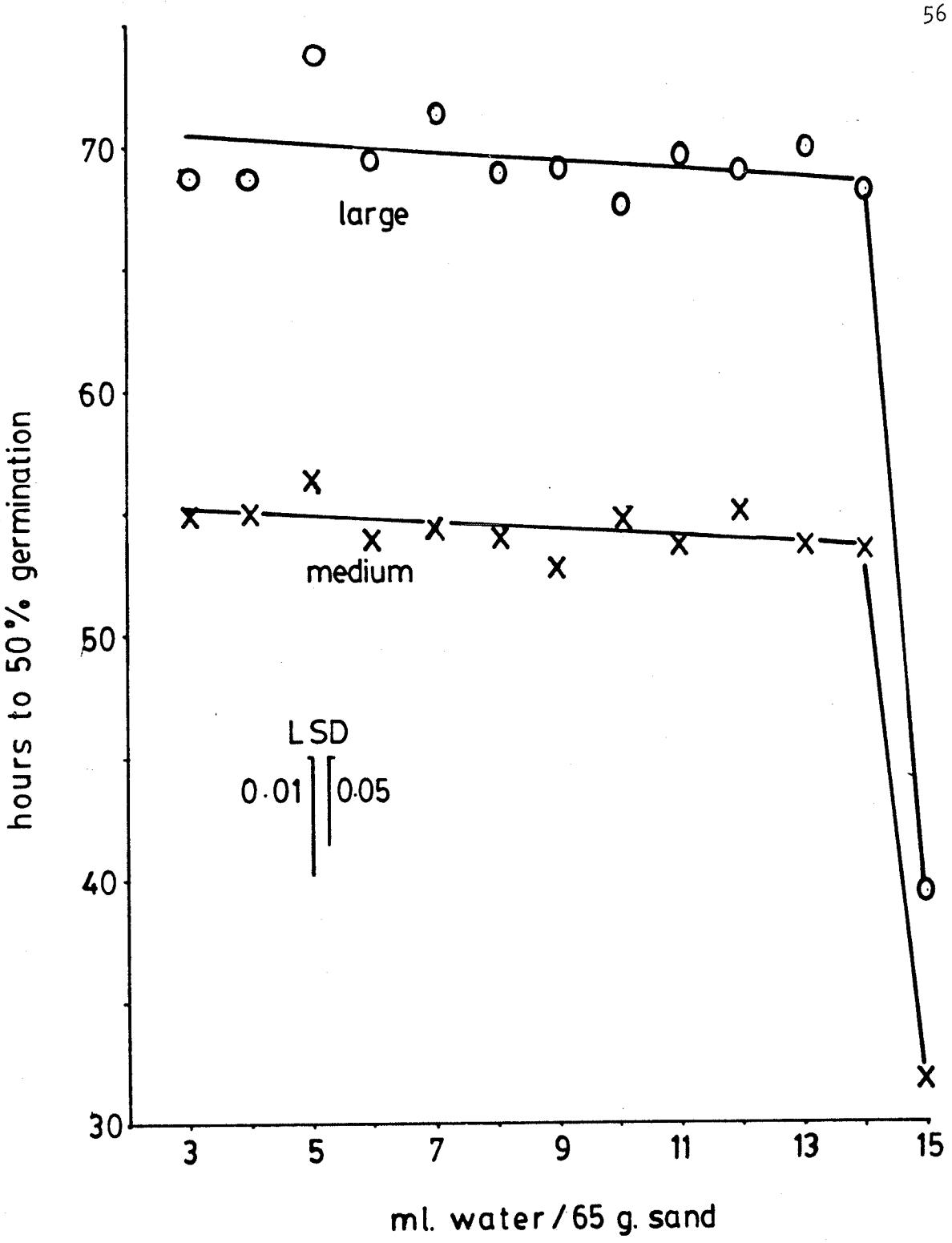


Fig. 2. Hours to 50% germination of two Neepawa seed sizes at various sand moisture levels. $L.S.D._{0.05} = 3.96$.

slightly with increased sand water, a result in agreement with many other studies (Bewley and Black, 1978).

The seed size - water interaction was the result of a varying gap in hours between the two seed sizes across the water range. Between 3 and 14 ml. medium seed reached 50% germination on the average more than 15 hours sooner than their large counterparts. However, at 15 ml. water (free liquid water) the difference was only half as great (7.6 hours).

5.3.2 Part B

Figure 3 shows the percentage germination of both coumarin treated and control seeds at 52 and 70 hours across the water range. Interestingly, the coumarin-treated seeds behaved very similarly to the control seeds in the drier conditions and only exhibited strong inhibitory effects under wet conditions where the seed was in contact with liquid water. Acetone control seeds (not shown), although they slightly delayed germination, behaved essentially as the control untreated seeds. If seeds were treated with lower concentrations of coumarin, the inhibitory effects at 15 ml. water were not as strong, or absent (data not shown). The response of coumarin here appears to be similar to that expressed by water sensitive seeds: Jansson (1959), found that water sensitivity could be induced in barley with added coumarin.

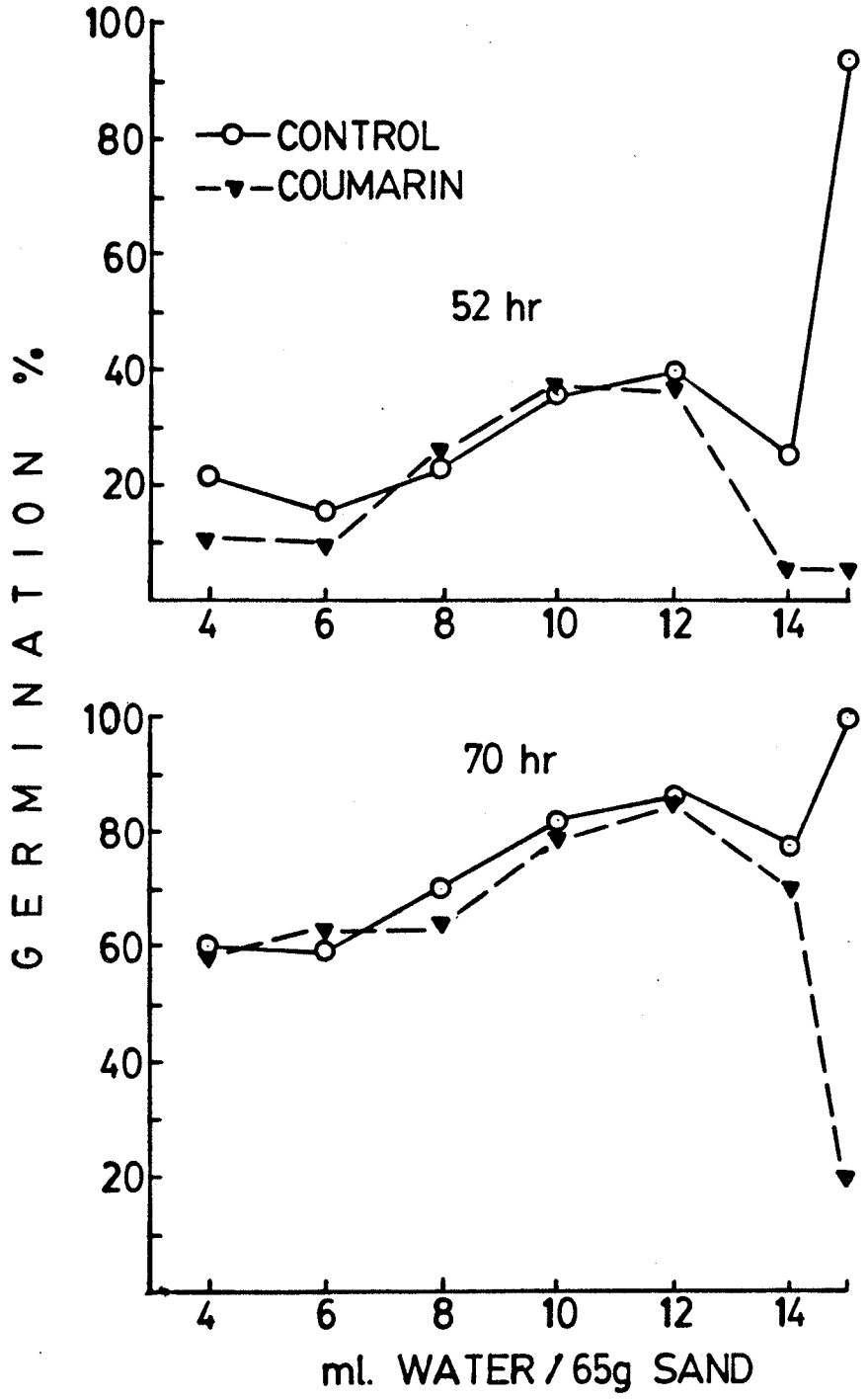


Fig. 3. The effect of coumarin on Neepawa germination at various sand water levels.

Chapter VI

EXPERIMENT III - SEEDING DENSITY - SEED SIZE

6.1 INTRODUCTION

An experiment was conducted to determine the hours to 50% germination as affected by four seeding densities of small and large sized Neepawa wheat. Shaykewich and Williams (1971b) demonstrated how increased seeding density decreased the water uptake rate and delayed germination in rapeseed.

6.2 MATERIALS AND METHODS

Sixty-five grams of fine silica sand and 10 ml. water were mixed and packed in 8.0 cm. diameter containers. The surface area of the sand on which the seeds germinated was therefore 50.3 cm. squared. The four seeding densities ranged from 0.5 to 4.0 seeds/cm. squared. The two lowest densities had either 25 or 50 seeds spread over the entire surface. The two highest densities had 50 seeds distributed over 1/2 or 1/4 of the surface area. The experiment, then, was a 2 x 4 completely randomized factorial. All of the treatments had 4 replicates except for the two lowest densi-

ties of large seed which had 8 replicates. The germination temperature was 15 C. Hours to 50% germination was calculated using linear regression on the points surrounding 50% germination. The harmonic mean was used in calculating the standard deviation and was determined to be 4.6.

6.3 RESULTS AND DISCUSSION

Both seeding density and seed size affected the hours to 50% germination (Appendix, Table 9). Higher densities, especially in the large seed, resulted in delayed germination. The treatment means as well as L.S.D. values are shown in Figure 4. The mean hours to 50% germination in all the small seed treatments was 49.4, while in the large seed, the value was 69.3 - a difference of about 20 hours. The effect of density was quite different between the two seed sizes. While in the small seed there was only a 6.3 hour delay between the highest and lowest density, the large seed treatment demonstrated an 18.5 hour delay, thus explaining the size-density interaction.

These results are quite easily explained in terms of water requirements. Small seeds obviously required less water to reach a given percentage water than large seeds. (Hadas, 1977; Muchena and Grogan, 1977)

High seeding densities forced seeds to compete for the same water. The small seeds required less water, so

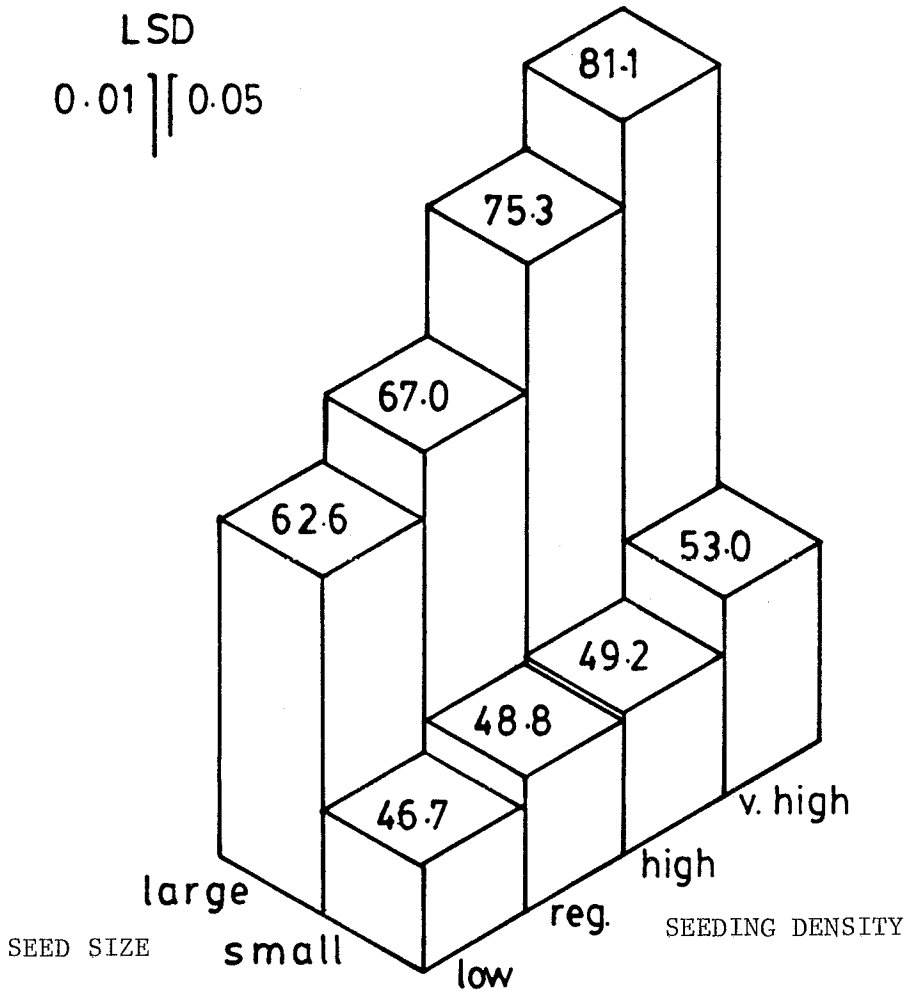


Fig. 4. The effect of seeding density and seed size on hours to 50% germination in Neepawa wheat. L.S.D.$_{0.05}$ = 4.00. Base value is 40 hours.

even at high densities, competition was minimal. High density large seedings resulted in much greater competition which, in turn resulted in a faster reduction in the external hydraulic conductivity (Shaykewich and Williams, 1971b).

A short-coming in the design of the experiment is evident at the two highest densities. In this case, 50 seeds were distributed only on one-half or one-quarter of the surface area. Seeds located at the boundary between the seeded and non-seeded regions could draw water from the non-seeded region with no competition. As such, the reported hours to 50% germination might be somewhat lower than they should be.

Chapter VII

EXPERIMENT IV - THE EFFECTS OF SEED PLACEMENT, CHEMICAL TREATMENT, AND SEED TYPE

7.1 INTRODUCTION

A study was conducted to determine the effects of seed placements on sand, seed size and type, coumarin treatment, and dormant seed, on hours to 50% germination and percent water at 50% germination. The study was divided into four sections, with a combination of some of the factors examined in each.

7.2 MATERIALS AND METHODS

7.2.1 Part A: The effect of position and chemical treatment on Neepawa wheat

A batch of large size Neepawa seeds was divided into three equal parts. One-third of the seed remained the untreated control, while the remaining two-thirds received a chemical treatment. Of primary interest was the effect of coumarin on water uptake and germination patterns, as coumarin is a well known germination inhibitor (Khan, 1977).

One-third of the seeds received a coumarin treatment by submersing seeds for exactly one hour in a solution con-

7.2.2 Part B: The effect of position and chemical treatment on Norstar wheat

An experiment almost identical to part A was conducted. The only difference was that medium-sized Norstar wheat was used. This, therefore, also was a 3 x 3 completely randomized factorial.

7.2.3 Part C: The effect of seed size and position on Neepawa wheat

The effects of seed size and placement were studied in this section. Two sizes of Neepawa wheat, medium and large, were germinated at the three positions. This resulted in a 2 x 3 completely randomized factorial. Four replicate values for the two dependent variables were determined. The data from the control seeds of Part A was used for the large seed data, and therefore is identical.

7.2.4 Part D: The effect of position and temperature on dormant Neepawa wheat

Two different samples of Neepawa seed containing natural post-harvest dormancy were obtained. Because of only a limited quantity, this seed was not fractioned into size or density groups.

As in Part A, 50 seeds were placed in the three positions and were germinated at two temperatures, 15 and 23 C for Sample I and 15 C for Sample II. Due to lack of seed, only two replicate values were obtained for both hours and water content at 50% germination in this 2 x 3 and 1 x 3 completely randomized factorial.

7.3 RESULTS

7.3.1 Part A: The effect of position and chemical treatment on Neepawa wheat

Both chemical seed treatments and seed positions showed significance in the F-test at p=0.01 for both dependent variables (hours and water content at 50% germination). No interactions were observed between chemical treatment and position at p=0.01 (Appendix, Table 10). The individual treatement means for each treatment and position combination along with L.S.D. values are shown in Figure 5 for hours and Figure 6 for water at 50% germination. When comparing each treatment mean, it was evident that embryo-down and control seeds germinated the fastest. Brush-down seeds germinated slightly faster than the surface seeds.

The coumarin treatment did not behave significantly differently from the acetone control and both reached 50% germination about 8 or 10 hours later than the untreated controls. Control seeds had a much lower water content than either coumarin or acetone treated seeds. These latter seeds had almost identical water contents at 50% germination at all positions. Surface seeds had the lowest and brush-down seeds had the highest water contents. One case, the embryo-down control, had a somewhat lower water value than the surface control, but the difference was not significant.

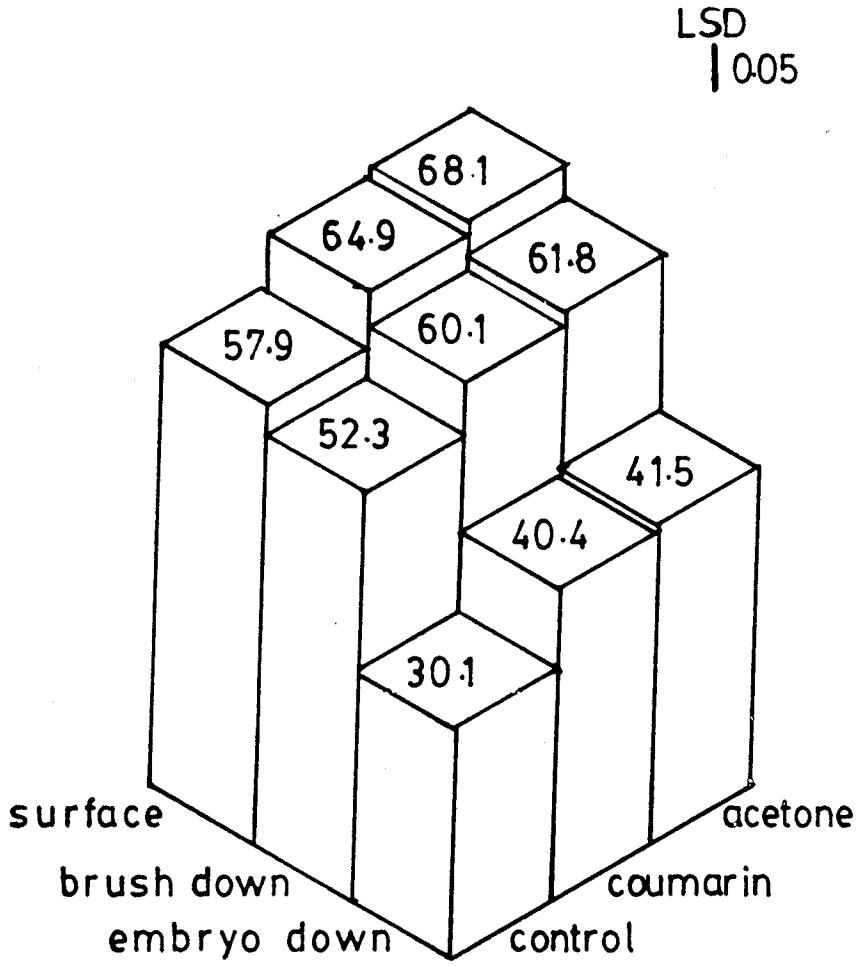


Fig. 5. The effect of seed position and treatment on hours to 50% germination in Neepawa wheat. $L.S.D._{0.05} = 5.92$.

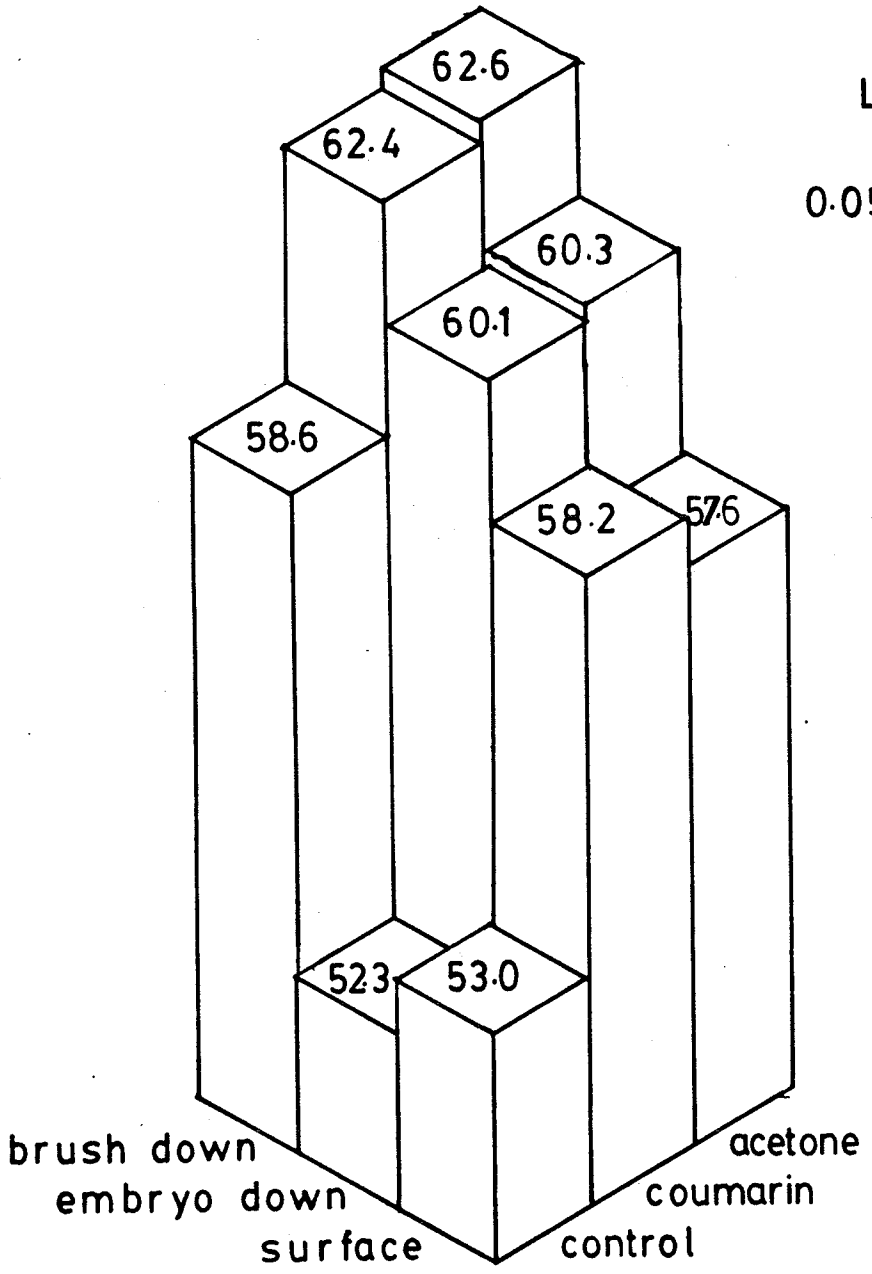


Fig. 6. The effect of seed position and treatment on the water content (d. w. basis) at 50% germination in Neepawa wheat. $L.S.D._{0.05}$ = 2.26. Base value is 50 %.

7.3.2 Part B: The effect of position and chemical treatment on Norstar wheat

Both chemical seed treatements and seed positions of the Norstar wheat showed significance in the F-test at p=0.01 for both dependent variables (hours and water content at 50% germination). No interactions were evident at p=0.01 (Appendix, Table 11).

The individual treatment means for each treatment and position combination along with L.S.D. values are shown in Figure 7 for hours and Figure 8 for water at 50% germination.

Embryo-down seeds consistently reached 50% germination sooner than the other two seed placements (Fig. 7). The brush-down seeds germinated slightly faster than the surface seeds. The untreated control seeds tended to germinate several hours earlier than the acetone and coumarin-acetone treatments. No significant time difference was observed between the acetone and coumarin treatments.

Untreated control and embryo-down seeds had the lowest water content at 50% germination. The coumarin-treated and brush-down seeds had the highest values (Fig. 8).

7.3.3 Part C: The effect of seed size and position on Neepawa wheat

In the F-test, only position significantly affected hours to 50% germination. Both size and position affected percent water at 50% germination (Appendix, Table 12). No

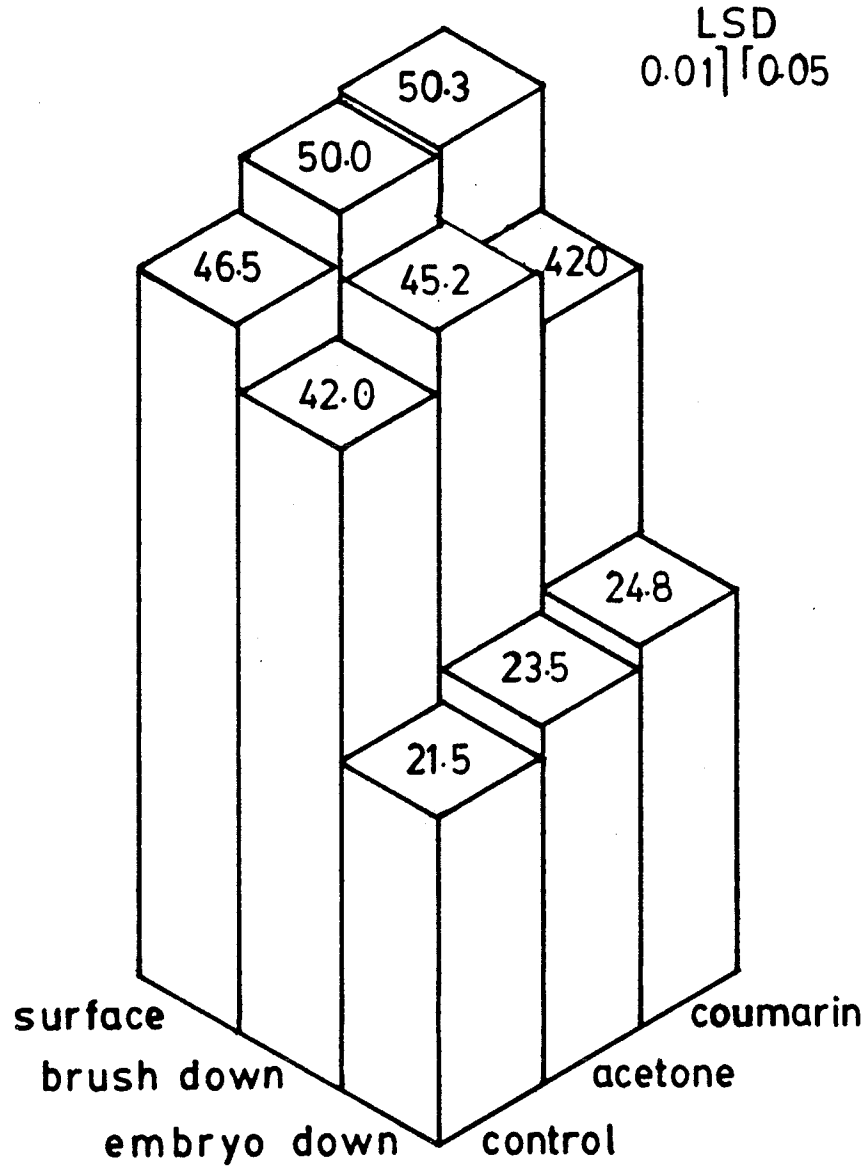


Fig. 7. The effect of seed position and treatment on hours to 50% germination in Norstar wheat. $L.S.D._{0.05} = 2.25$.

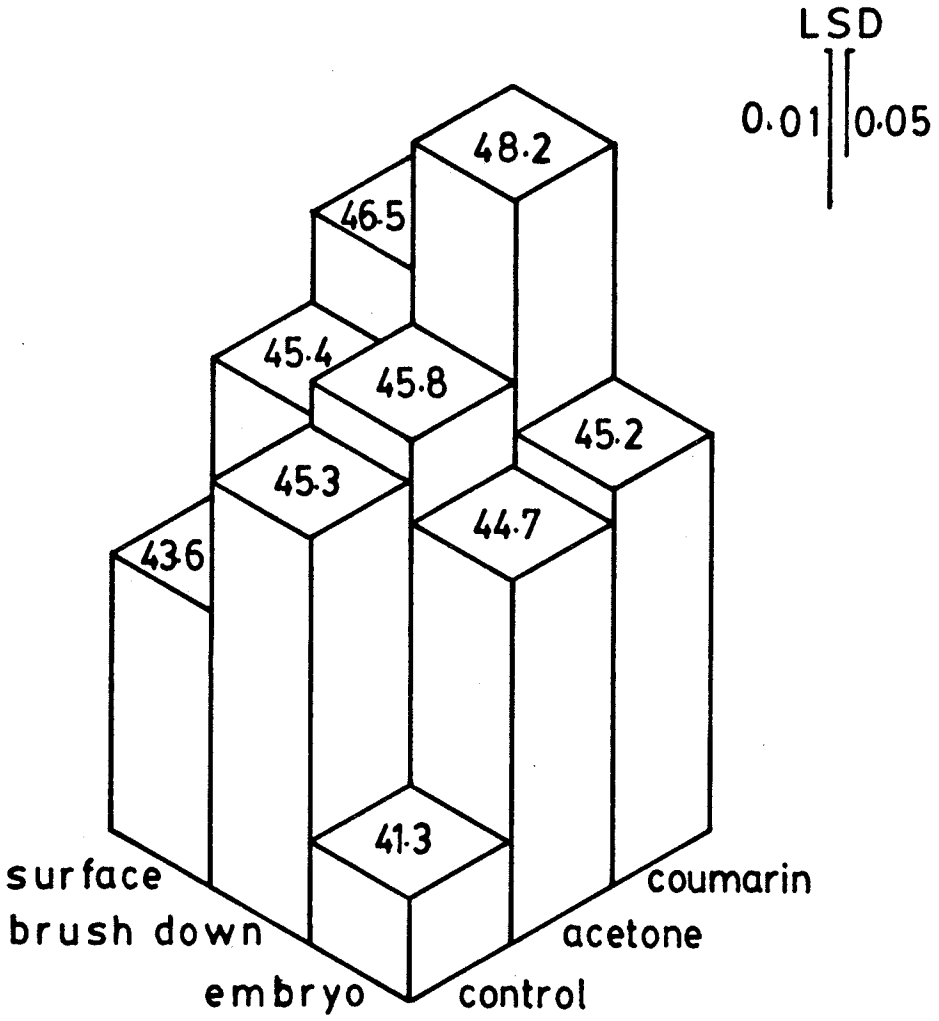


Fig. 8. The effect of seed position and treatment on water % (d. w. basis) in Norstar wheat. $L.S.D._{0.05} = 1.40$. Base value is 40%.

interactions were observed. The individual treatment means are shown in Figs. 9 and 10.

As before, the embryo-down seeds germinated well ahead of the other two placements. Although there was no significant difference between the two, surface seeds always took slightly longer to germinate than brush-down seeds. Size did not show significance in the F-test. However, when observing individual treatment means, although brush and embryo-down did not show size effects, the surface medium seeds reached 50% germination over 3 hours sooner than the large seeds. This is in agreement with the size effects of surface-placed seeds in other experiments.

Embryo-down and surface-placed seeds had very similar water contents which were quite a bit lower than those observed in the brush-down seeds. The large seeds appeared to have lower water values even though significant differences were not observed at the surface and brush-down positions.

7.3.4 Part D: The effect of position and temperature on dormant Neepawa wheat

Both temperature and seed placement significantly affected hours to 50% germination and water content at 50% germination at $p=0.01$ (Appendix, Table 13). No interactions between the temperature and placement were evident in Sample 1.

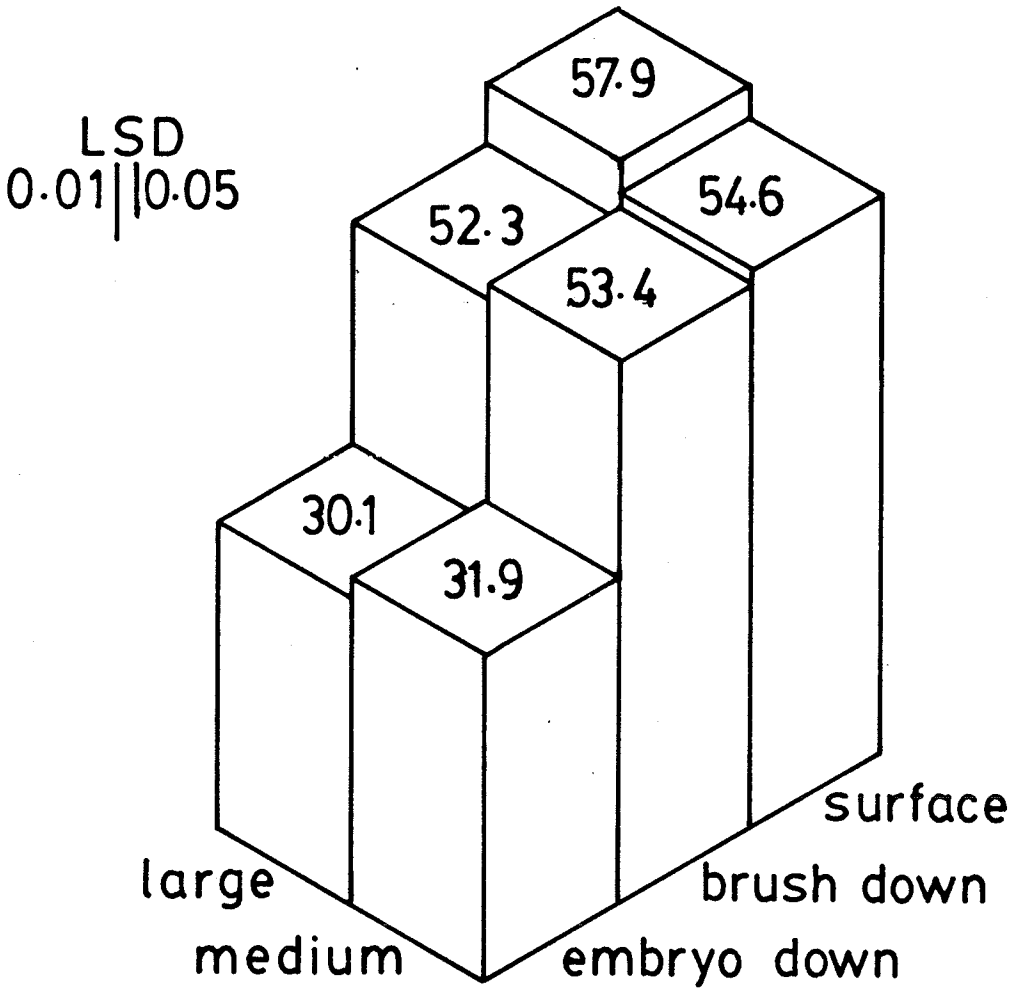


Fig. 9. The effect of seed position and size on hours to 50% germination in Neepawa wheat. $L.S.D._{0.05} = 5.49$.

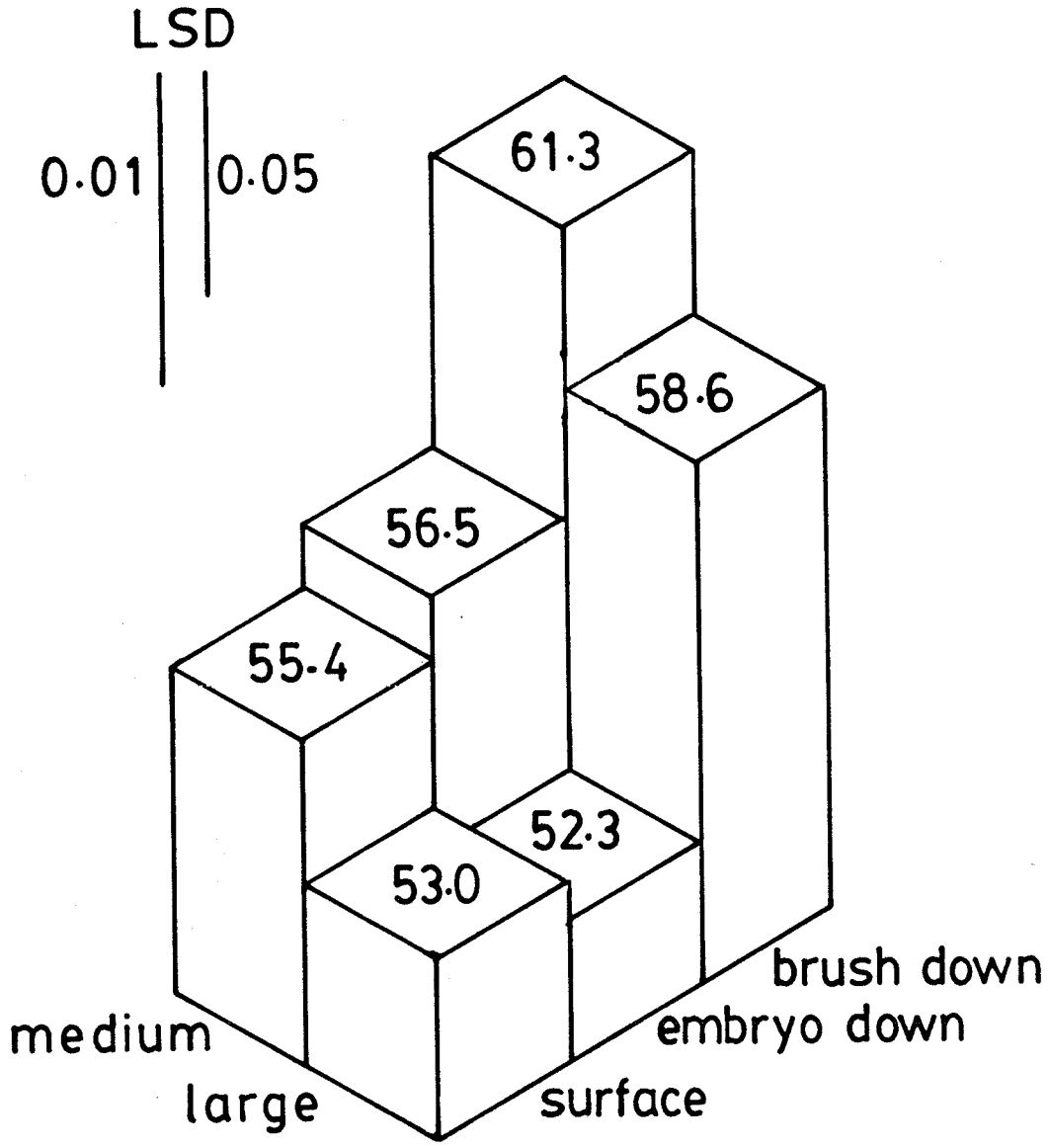


Fig. 10. The effect of seed position and size on water % (d. w. basis) in Neepawa wheat. $L.S.D._{0.05} = 3.72$.

In Sample I, the 23 C seeds germinated about 9 hours faster than the 15 C. seeds did, at all placements (Fig. 11). Again the embryo-down seeds were by far the quickest to reach 50% germination among the three placements. Although there was no significant difference between them, the surface treatments reached 50% germination by an average of two hours later than the brush-down in Sample I. However, in Sample II, the brush-down seed showed a great delay.

The 15 C temperature and the surface placement resulted in the lowest percent water content at 50% germination. Although there was no significant difference between them, the mean brush-down value was over 2% greater than that of the embryo-down (Fig. 12).

7.4 DISCUSSION

The effects of seed placement could have expressed themselves in various ways. Sand-seed contact area which is a factor in determining uptake (Collis-George & Hector, 1966), was obviously much less in the surface-placed seed than in the two other placements. The lower water uptake rate generally associated with the surface-placed seeds would explain the delayed germination and lower water content at 50% germination when compared to the other placements. The relatively low water content at 50% germination in surface seeds possibly was due to greater water equilib-

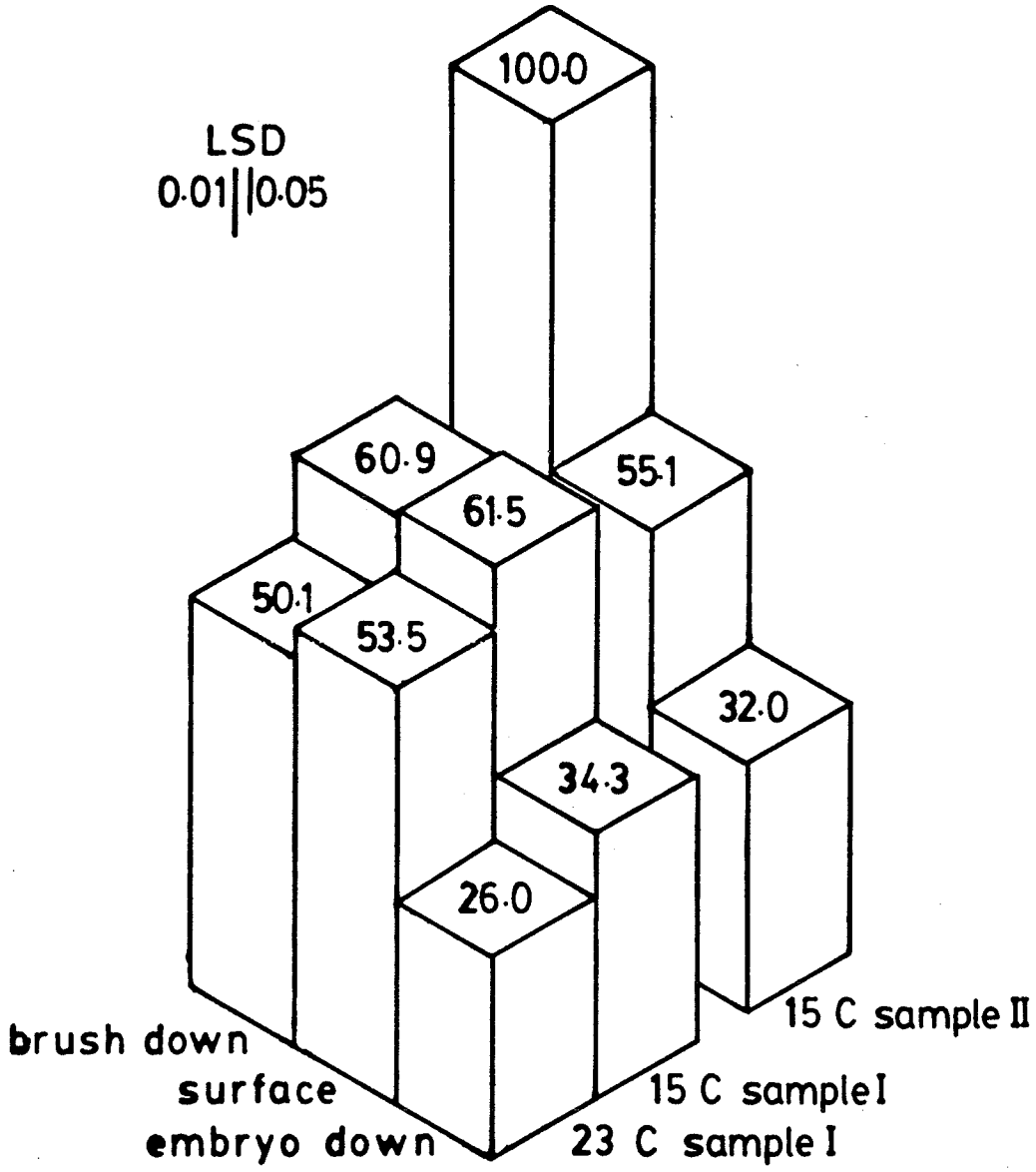


Fig. 11. The effect of seed position and temperature on hours to 50% germination in post-harvest dormant Neepawa wheat.

L.S.D.$_{0.05}$ = 6.05.

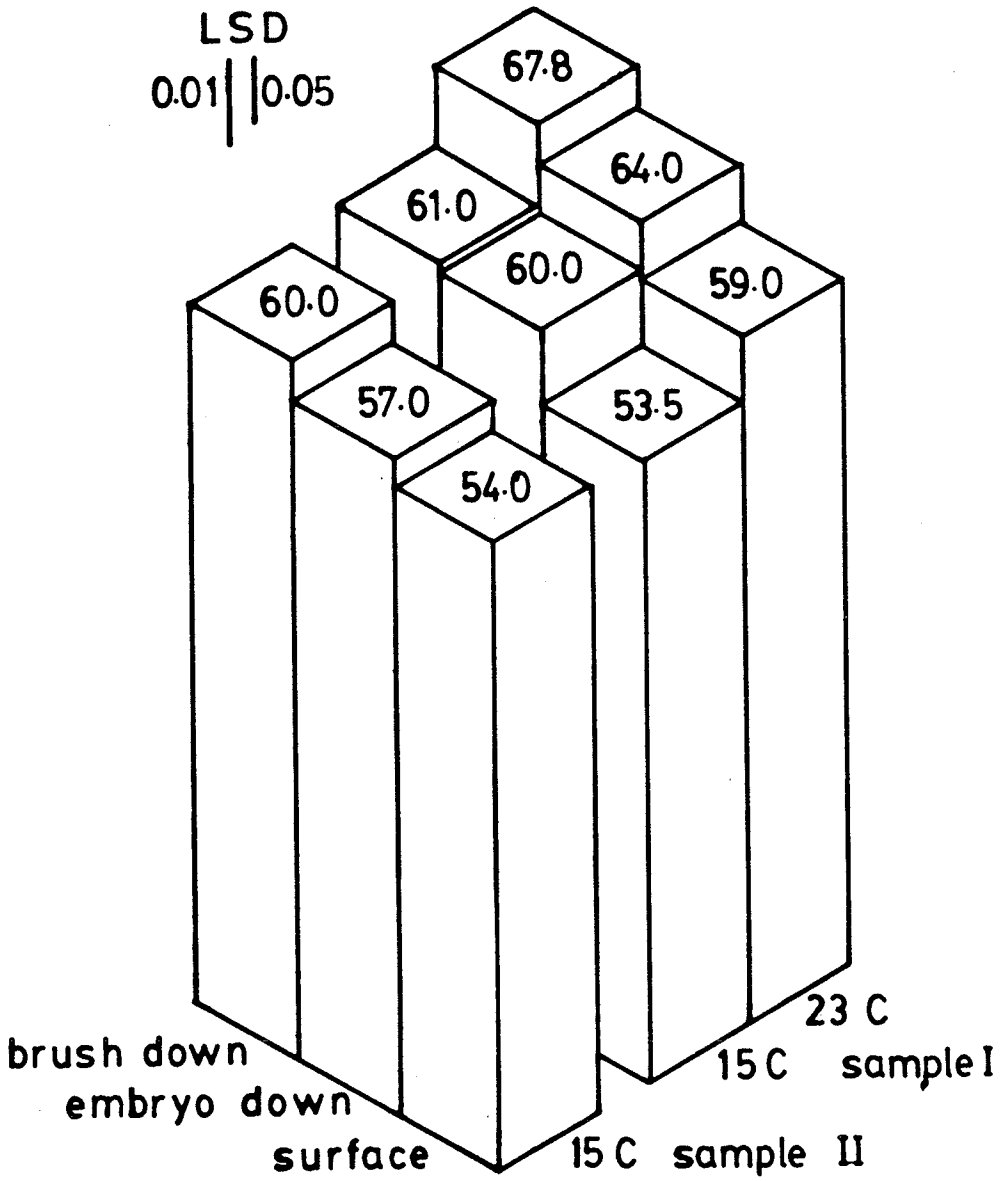


Fig. 12. The effect of seed position and temperature on % water (d. w. basis) at 50% germination in post-harvest dormant Neepawa. $L.S.D._{0.05} = 5.20$.

rium. Embryo-down seeds germinated rapidly because of the short water path to the embryo. In normal conditions, the embryo takes up water faster than the endosperm (Stenvert and Kingswood, 1976; Briggs, 1978). No inhibition of germination caused by the sands mechanical strength (Collis-George and Williams, 1968) was evident in the embryo-down seeds. Despite the fact that brush-down seeds had a relatively high contact area with the sand, time to 50% germination took almost as long as with the surface-placed seeds. Brush-down seeds had the highest water content at 50% germination of all placements. This would suggest that the water in brush-down seeds was in the wrong location for optimal germination.

Although the brush-down placement resulted in the highest water content for both Neepawa and Norstar seeds, the lowest water contents differed, and were surface and embryo-down, respectively. This difference could be related to the water movement and requirements of the wheats. In all cases, the Norstar germinated at much shorter times and lower water contents than the Neepawa. Possibly, the Neepawa required more endosperm water, or the water movement in the endosperm was more restricted than in the Norstar. The slower water uptake associated with surface-positioned seeds would result in greater water equilibrium through the seed and hence greater endosperm water content. In the case of embryo-down Neepawa, by the time the endosperm was suffi-

ciently hydrated, total uptake would have overshot the requirement if the seed was more at equilibrium (i.e., surface placement).

In both wheats, the acetone and coumarin (in acetone) resulted in somewhat of a delay. This most likely had something to do with effects of acetone on the seeds. Since both acetone and coumarin treatments resulted in higher water contents at 50% germination, possibly water entry and movement was redirected, resulting in a less efficient and hence higher water requirement. Possibly acetone soaking caused a relocation of surface waxes or phenols to the capillary space beneath the pericarp or in some other way affected the microstructure. The reason the coumarin treatment did not show much of an effect can be explained in terms of the results observed in Experiment 2, where strong inhibitory effects only expressed themselves when seeds were in contact with liquid water.

Seed size only affected surface-placed seed with smaller seeds germinating earlier. With seeds pushed into the sand, no significant differences were observed. Hadas (1977) noticed no seed size effects if seeds were in good contact with soil particles. With a low contact area, differences in germination water requirements between sizes would result in amplified delays in larger seeds.

When the 15 C dormant Neepawa seeds in Part D, except for Sample II brush-down, are compared to the non-dor-

mant untreated ones in Part A, it becomes evident that at all placements, the dormancy resulted in a slight delay to 50% germination, suggesting that the effect of dormancy at the temperature was not that great. The Sample II brush-down seeds showed strong inhibitory effects. Possibly water moving along the pericarp was transporting inhibitor to the embryo, or the pericarp had not dried out to the same extent affecting the inhibitor status (Evans, et al., 1975).

The surface data of the dormant seeds (Part D) can be compared to the results in Experiment VI to include the effect of temperature on the germinability of the dormant seed. In Experiment VI, the mean hours to and water content at 50% germination of the non-dormant Neepawa at 15 and 23 C was 61 and 35 hours at 58.6 and 56.5% water respectively. The surface results of the dormant seed (Part D) had values of 58.5 and 53.5 hours and 53.8 and 59.0% water respectively for 15 and 23 C. These results indicate that the dormancy only really expressed itself in delayed germination at 23 C and not 15 C. Similarly, Mackey (1976) and Gosling et al (1981) also observed seeds which only expressed dormancy at warmer temperatures.

Table 1 shows average water uptake rates from seeding to 50% germination. It demonstrates that both non-dormant and dormant seeds had similar uptake levels at a given seed placement at 15 C, except for dormant Sample II brush-down seeds. Surface uptake was slowest, while embryo-down

uptake was most rapid. The slow uptake associated with surface seeds can be explained by a low seed-sand contact area. The rapid uptake of embryo-down seeds was likely due to rapid uptake at the micropylar end (Brown, 1907; Collins, 1918; Blacklow, 1972; Stewart & Kingswood, 1976). The 23 C results prove to be interesting. Although in both non-dormant and dormant seed, the uptake rates were both higher than at 15 C, the non-dormant seed appeared to have a substantially higher uptake rate than the dormant seed (at least on the surface placement). This would suggest that the expression of dormancy at 23 C is related to lower water uptake rates.

TABLE 1

Neepawa Wheat Water Uptake Rates (percent water per hour)*

	Exp. VI Average 15 C.	Exp. IVA&C Large 15 C.	Exp. IVC Medium 15 C.	Exp.VI Average 23 C.
Surface	0.78	0.73	0.81	1.34
Brush-down	-	0.91	0.94	-
Embryo-down	-	1.37	1.43	-

	Exp.IVD Average Dormant I 15 C.	Exp.IVD Ungraded Dormant II 15 C.	Exp. IVD Ungraded Dormant I 23 C.
Surface	0.69	0.78	0.91
Brush-down	0.82	0.49	1.13
Embryo-down	1.43	1.44	2.04

* The initial 11% water was subtracted. The rate is the average from seeding time to 50% germination expressed in percent water (d.w. basis) per hour.

Chapter VIII

EXPERIMENT V: WATER UPTAKE AND GERMINATION - TEMPERATURE GRADIENT TABLE

8.1 INTRODUCTION

A temperature gradient table was used to enable the simultaneous germination of seeds across a range of temperatures. Two dependent variables, hours to 50% germination, and percent water at 50% germination were determined.

8.2 MATERIALS AND METHODS

8.2.1 Temperature Gradient Table construction

A temperature gradient table was constructed using many ideas from the gradient table constructed by Clegg and Easton (1978). The table surface consisted of a 35 x 56 cm. aluminum plate 0.5 cm. thick. Under both of the 56 cm. edges, a thin brass plate 56 x 6 cm. was attached. This plate had 9 mm. copper tubing bent in a "U" shape soldered unto its surface. Temperature controlled water passed through this tubing, thereby determining the temperature of the aluminum plate at that particular end. At one edge, cold water and at the other edge warm water passed through the tubing. This created a temperature gradient across the 35 cm. width of the plate. The temperatures across the plate were tested

periodically using thermocouple thermometers. Temperatures were directly related to the distance from the two extreme temperature edges and ranged from 13 to 23 C. The change was linear so that the temperature at the mid-point was 18 C. At a given location, temperature was almost uniform varying only +/- 0.25 C. To eliminate external factors, the whole table was insulated by a styrofoam box (R=7.5).

8.2.2 Container size, placement, temperature, and preparation

The containers used to hold the sand water mix were rectangular (6 x 11 cm.) and 5 cm. high. They were placed parallel to the gradient edges, so that only the 6 cm. width experienced a temperature gradient. For this reason, a +/- 0.86 C deviation from the center of the container occurred. Ideally, narrower containers should have been used in order to minimize temperature variation within a container.

It was important that all containers were properly sealed to prevent water vapour movement from warm to cold areas. In a preliminary experiment, in which containers were left open, water moved rapidly from warm to cold regions where it condensed. The sand in the warm end dried out very rapidly.

Due to a larger surface area (11 x 6 = 66 cm. squared), and an attempt to reduce surface temperature variation by using a thicker sand layer, 150 gm. of fine silica sand were mixed with 25 ml. of water resulting in a 0.1667

water/sand ratio. The sand was packed using a 1 kg. weight dropped from a 10 cm. height (as in experiment 1). One hundred seeds were placed on the sand surface distributed evenly.

8.2.3 Calculations of Hours to 50% Germination and percent water at 50% germination

In order to measure water uptake with time, seeds were periodically removed from the containers for weighing and then quickly returned to the containers to continue taking up water. The degree of germination was also determined. The whole procedure was repeated 4 to 6 times until percent germination exceeded 50%. It was assumed that any increase (or decrease) in weight was solely the result of a change in the seeds' water status. The coldest seeds had to be blotted dry prior to weighing, as they quickly had water condense on them when exposed to room temperature. Another problem was that small amounts of sand tended to stick to the seeds. As much sand as possible was removed from the seeds by a quick pass-over window screening. Although not all the sand was removed, the few grains of sand which remained were not numerous enough to greatly affect the percent water content calculations. Of greater consequence, perhaps, was the fact that seeds were not returned to their exact previous location after being weighed. Since seeds removed water from the sand closest to them, relocation upon weighing would most likely have put them on locations from which water had not yet been withdrawn.

After the final wet weighing (at which time germination exceeded 50%), the seeds were placed into an 90 C drying oven for at least 24 hours and reweighed to obtain the oven dry weight. This oven dry value was used in calculating percent water content. The formula used was (wet wt. - oven dry wt.)/oven dry wt. x 100. In a given container, hours to 50% germination was calculated using linear regression between the values surrounding 50% germination. This resulting hour value was then used on the percent water data, and again linear regression was used in a similar fashion to determine percent water at 50% germination.

8.2.4 Experiment

A 2 x 5 factorial completely randomized designed experiment was conducted on the germination table. Two seed sizes, medium and large, were germinated at 5 different temperatures (13, 15.5, 18, 20.5, and 23 C). The medium seed was replicated 7 times while the large seed had 4 replicates.

8.3 RESULTS AND DISCUSSION

Both seed size and temperature showed significance at p=0.01 in determining hours to 50% germination. Only temperature influenced the percent water content at 50% germination. No significant interactions were observed (Appendix, Table 14).

Warmer temperatures greatly speeded up germination. Seeds germinated at 13 C took about three times as long to reach 50% germination than those at 23 C. In both seed sizes, at each successive decrease in temperature, the increase in delay became larger, especially from 15.5 to 13 C (Fig. 13). Large sized seed reached 50% germination by an average of 14 hours later than medium sized seed. This delay amounted to about 10 hours at the three warmest temperatures, but increased to 17 and 22 hours at 15.5 and 13 C respectively.

Water content at 50% germination increased with temperature, and ranged from 55.4 to 63.5%. The change was fairly linear with temperature (Fig. 14).

Although seed size did not significantly affect the percent water at 50% germination, the medium sized seed had the higher values at temperatures from 13 to 18 while the large seed had higher values at the two warmest temperatures (Fig. 14). No significant interactions were observed.

An explanation for the increased water contents at higher temperatures involves greater water uptake rates in warmer conditions (Mohsenin 1970) and seed relocation. Even though seeds might have reached the critical minimum water content, they did not necessarily germinate immediately. Possibly seed water was not at the right locations for germination. Given that seeds were repositioned to areas with high hydraulic conductivity regularly, uptake was allowed to

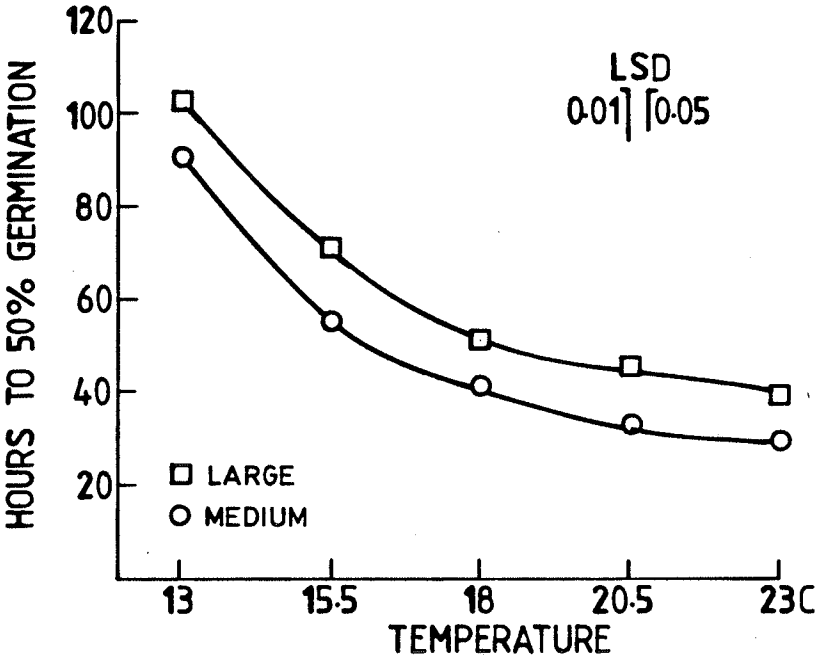


Fig. 13. Hours to 50% germination of two Neepawa seed sizes, $L.S.D._{0.05} = 8.96$.

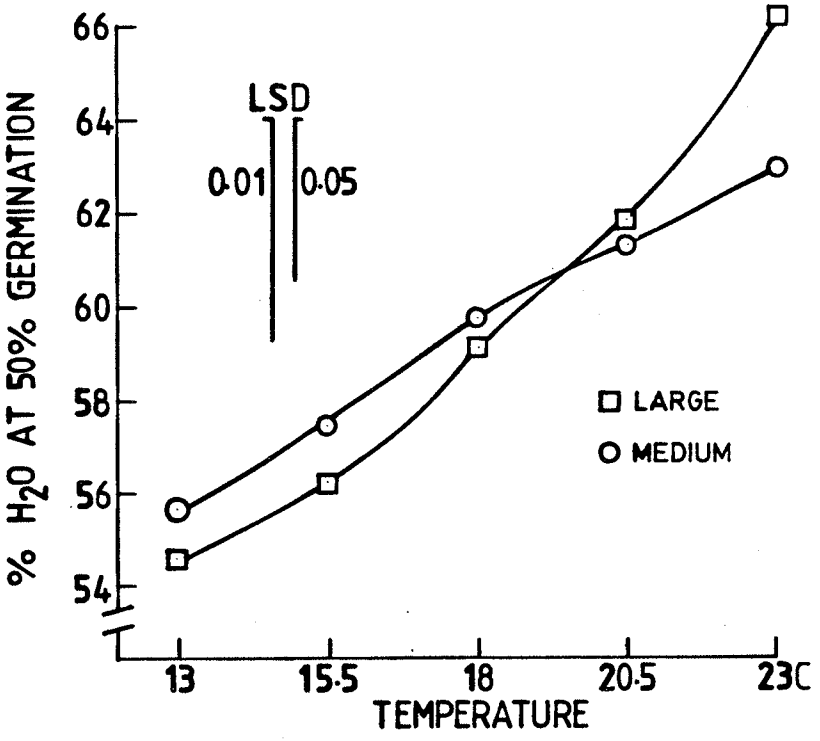


Fig. 14. Water % (d. w. basis) at 50% germination of two Neepawa seed sizes, $L.S.D._{0.05} = 3.45$.

be relatively rapid until germination. Because of this, seeds might have had a greater tendency to water movement in the free rather than bound form (Becker and Sallans, 1956).

Chapter IX

EXPERIMENT VI - WATER UPTAKE AND GERMINATION - GERMINATION CABINETS

9.1 INTRODUCTION

An extensive study was conducted to examine the effects of seed size, temperature, and sand water supply on the water uptake and germination characteristics of Neepawa and Norstar wheat. Of interest were six different dependent variables: lag time, rate of germination after the lag time, hours to 50% germination, percent water content at the end of lag time, rate of water uptake after lag time, and percent water content at 50% germination. The experiment was divided into two subsections. Section A involved three different seed sizes of Neepawa wheat while Section B had one size of Norstar wheat.

9.2 MATERIALS AND METHODS

9.2.1 Part A - Neepawa

The procedure began by placing 50 Neepawa seeds on the sand surface of a 8.0 cm. diameter container containing 65 gm. of packed fine silica sand (as in experiment 1) mixed with either 3 or 10 ml. water. The seeds were evently distributed over the entire sand surface, resulting in an aver-

age seeding density of 1.0 cm. squared per seed. The containers were placed in temperature controlled germination cabinets.

Containers were removed periodically at which time both percent germination and percent water content were determined.

Unlike similar experiments using the temperature gradient table, where seeds were returned to the containers so that further data on those particular seeds could be collected, this experiment was conducted in a destructive manner. Enough containers of a given treatment (usually 16 to 20) were set up, so that two replicate containers could be removed at regular intervals throughout the whole germination period (8 to 10 times). Warm temperatures which had a shorter duration of the experiment had the lower number of containers.

The majority of the 8 to 10 sampling times occurred between the end of the lag period (beginning of germination) and about 70% germination.

This procedure was conducted for three seed sizes (ML = medium light, MD = medium dense, L = large) at four temperatures (8 C, 12 C, 15 C, 23 C), and at two sand water levels (3 ml. and 10 ml. water per 65 gm. fine silica sand). The experiment was a completely randomized 3 x 4 x 2 factorial experiment. Over 430 containers with seed were set up for all of the 24 different treatments.

Each time a container was removed from the germination cabainet, the number of germinated seeds was quickly determined. The seeds were placed in previously weighed metal drying containers, and weighed to determine the wet weight. After drying at 90 C for at least 24 hours, the containers were again weighed to determine the oven dry seed weights. Sand particles which had stuck on to the seeds at the initial removal from the germination container lost all attraction to seeds after drying. Using metal window screening, it was easily removed, and the oven dry seeds were reweighed. Thus, the weight of the sand was calculated. This value was subtracted from the previous wet seed weight to give the accurate wet seed weight. Thus the moisture content of the seeds (oven dry basis) at the time of removal from the germination container was calculated by the formula: percent water = [(wet wt.-sand)-(dry wt.-sand)/(dry wt.-sand)] x 100.

9.2.1.1 Calculation of Germination and Water Uptake

The germination response of a normal population of seeds consists of a lag period followed by a sigmoid germination of the population (Bewley and Black, 1978). The lag period is defined as the time between seeding and the beginnings of germination.

When the data points were plotted, the sigmoid curve contained a long central linear region. The best fitting

line was calculated by using data in which germination was greater than 4% but less than 90%. It was determined that values below 4% or greater than 90% did not fall in the linear portion of the curve, but were in the curved tail regions. Using GLM, linear regression obtained the best fitting line for all the points between 4 and 90% germination. The slope of this line consequently represented the post lag germination rate, while the point where this line intercepted the hours axis at 0% germination represented the lag time. Thus it was easy to calculate hours to 50% germination.

The percent water values were similarly treated. Water uptake with time was rapid initially, but levelled off and did not pick up appreciably until radicle growth was advanced. Uptake between 4% and 90% germination was linear, and therefore linear regression was also used here to caluclate the best fitting line. Using the hour values of 0% germination (end of lag) and 50% germination, the water contents at these times were calculated. The slope represented the rate of water uptake during the germination phase.

For each of the 24 different treatments, regression lines were calculated for both germination and water. There were two replicates per treatment, with the average number of points per replicate at 13.

9.2.2 Part B - Norstar

An experiment very similar to part A was conducted with medium-sized Norstar wheat. The four temperatures (8, 12, 15, and 23 C) and two sand water levels (3 and 10 ml.) resulted in a 4 x 2 completely randomized factorial experiment. The procedure in setting up the experiment, collecting, and analyzing the data was identical to that in the Neepawa experiment (part A).

9.3 RESULTS

9.3.1 R-square values

Both part A and B r-square values for all the lines generated are shown in Appendix Tables 15 and 16 respectively.

Generally, higher r-square values were generated for germination hours than for water content. Both variables tended to have higher r-square values at warmer temperatures.

9.3.2 Lag-Time (Neepawa)

Increased seed size, lower temperature, and drier sand resulted in a longer lag period (Appendix, Table 17, Fig. 15). The overall mean lag times for the large, medium dense, and medium light seeds was 59.5, 48.5, and 44.5 hours respectively. As temperature decreased from 23 to 8 C, there was a three-fold increase in lag time. The wet 10 ml.

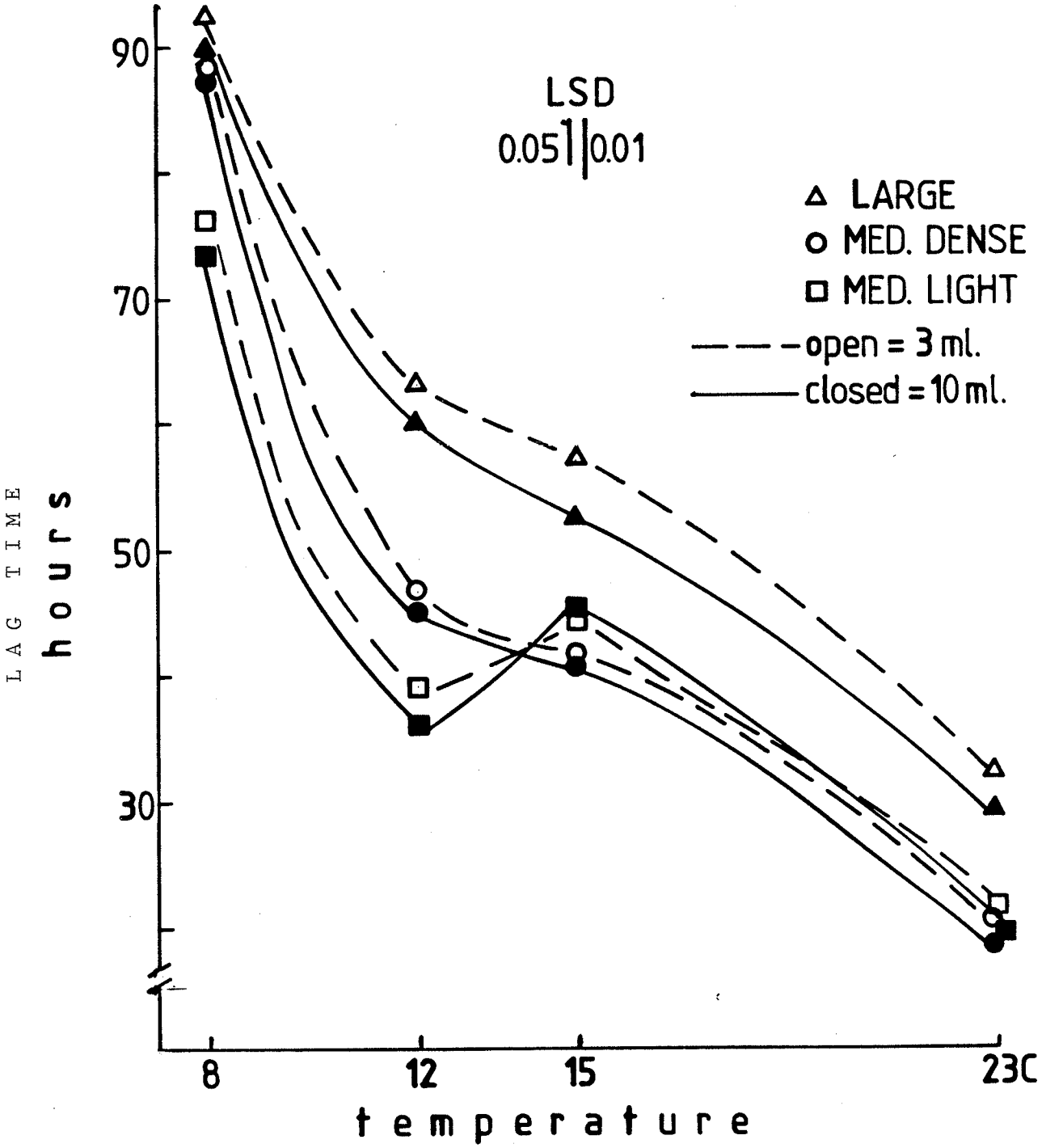


Fig. 15. Lag time (Neepawa). L.S.D.$_{0.05}$ = 3.52.

containers had an average lag time two hours shorter than the dry 3 ml. containers. A seed-size temperature interaction was present. This involved irregular behaviour of medium light seed at 15 and 23 C where lag time was greater than that of medium dense seed.

9.3.3 Post-Lag Rate of Germination (Neepawa)

Both seed size and temperature affected the post-lag rate of germination (calculated from the linear portion of the sigmoid germination curve). As well, an interaction existed between these factors. The two different water levels in the sand did not show a significant effect (Appendix, Table 18). Rates varied from a slow 1.35 hours/seed to 0.45 hours/seed (Fig. 16).

Both large and medium dense seed showed the slowest rate at 12 C, and the most rapid at 23 C. The 8 C rates were quite rapid relative to the 12 C values, but these were offset by much larger lag values, so that 8 C hours to 50 percent germination were still well behind those of 12 C.

All three seed sizes showed similar behaviour between 12 and 23 C. However, at 8 C the medium light seed had a much slower rate of germination. This resulted in a higher than expected hours to 50% germination at 8 C.

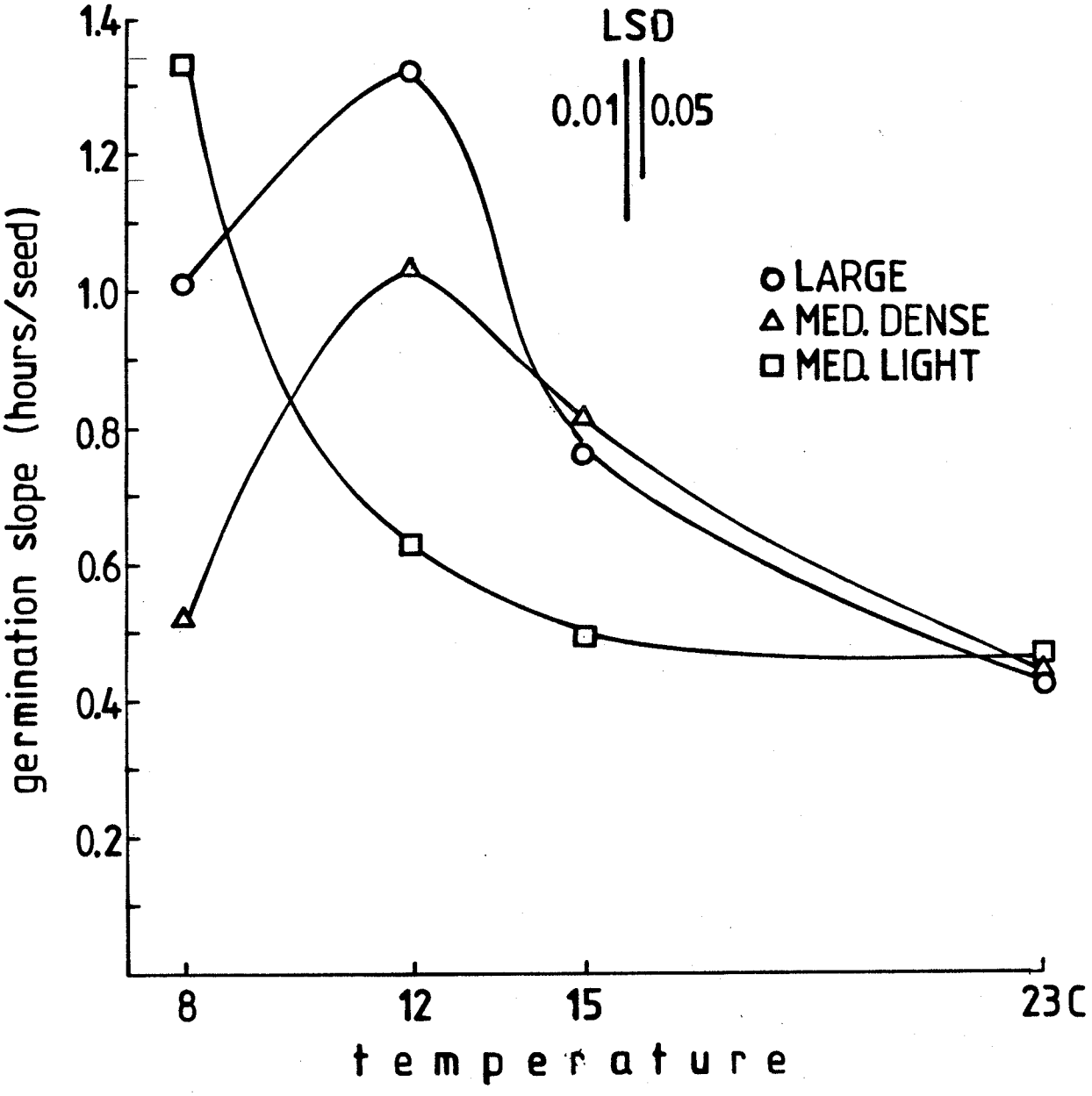


Fig. 16. Germination rate (Neepawa). $L.S.D._{0.05} = 0.173$.

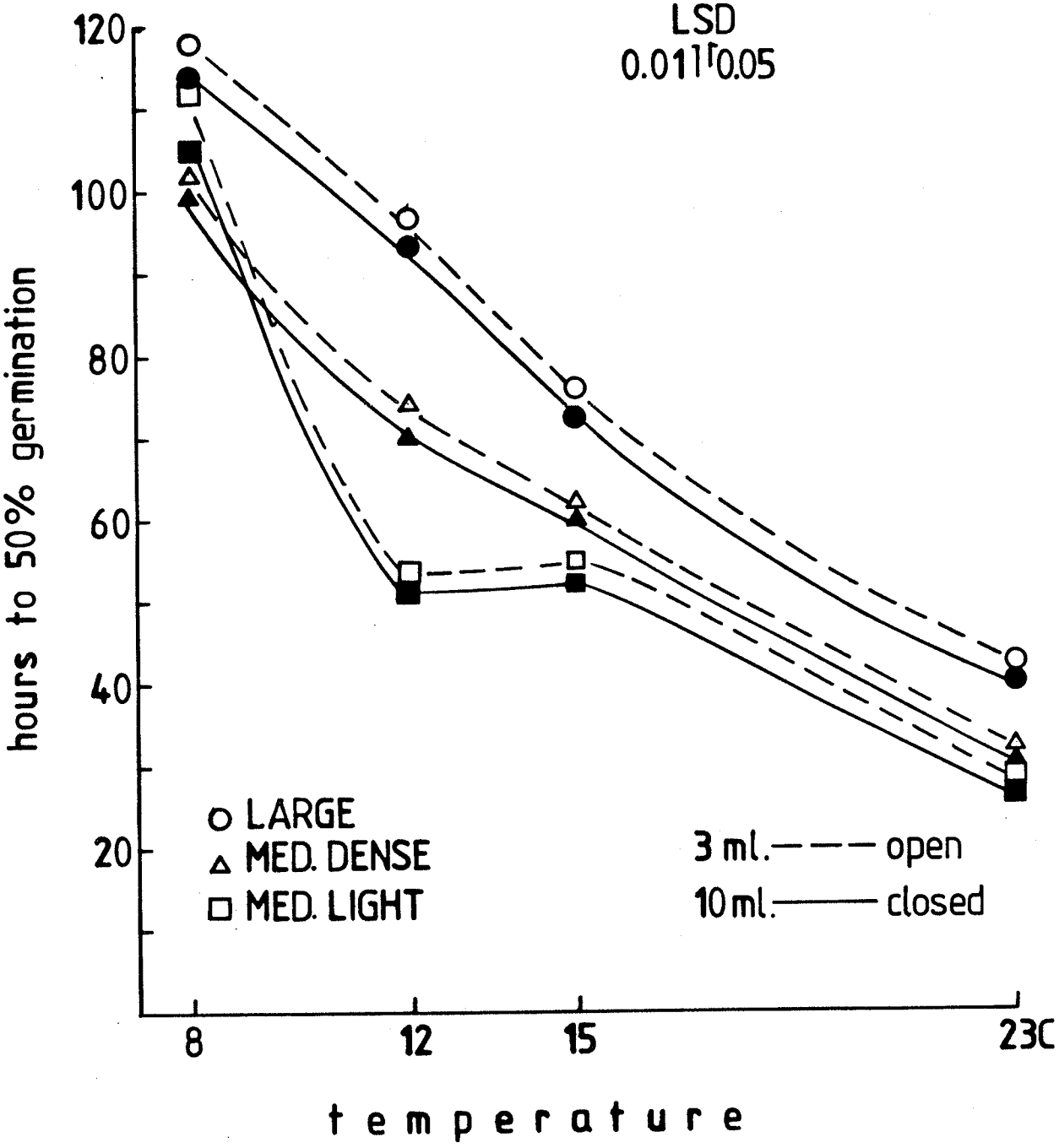


Fig. 17. Hours to 50% germination (Neepawa). $L.S.D._{0.05} = 2.58$.

9.3.4 Hours to 50% germination (Neepawa)

Hours to 50% germination was affected by seed size, temperature, and sand water, as well as several interactions of these (see Appendix, Table 19, Fig. 17). Warmer temperatures, and wetter sand caused smaller seeds, to reach 50% germination sooner. Both medium dense and large seeds formed fairly linear and parallel lines across the temperature range. However, the medium light seed showed irregular behaviour at 8 C and 12 C, a situation which resulted in a seed-size temperature interaction. A water-temperature interaction was present at p=0.05 but not at p=0.01. This was the result of smaller differences between 3 and 10 ml. treatments at warm temperatures compared to cold temperatures.

9.3.5 Percent Water at the End of the Lag (Neepawa)

Temperature and seed size affected the percent water at the end of the lag period, whereas no significant difference was observed between the two water treatments (Appendix, Table 20).

Temperature showed the most dramatic and consistent effect, with higher temperatures resulting in lower percent water values. The overall mean at 8 C was 58.4 percent water, while the 23 C mean was 50.9 percent. Possibly this drop at warmer temperatures was associated with water being present where needed for germination. If, under warm condi-

tions, water was more at equilibrium, p-amylase production and transfer to the embryo could occur more readily. The effect of temperature was much more pronounced between 8 and 15 C than between 15 and 23 C.

The effect of size was not consistent (see Fig. 18). However, larger seeds tended to have lower percent water values. The overall means for medium light, medium dense and large seeds were 54.2, 54.0, and 52.8 percent respectively. The size-temperature interaction was the result of the medium dense seed not following the normal pattern of the other two seed sizes.

Although there was no significance between the two water treatments the overall 10 ml. mean (53.9%) was 0.4% higher than the overall 3 ml. mean (53.5%).

9.3.6 Post-Lag Water Uptake Slope (Neepawa)

Both warmer temperatures and smaller seed size resulted in more rapid uptake rates (percent water d.w. basis/hour) (Appendix, Table 21). An interaction between size and temperature was the result of the large and medium dense seed curves crossing (see Fig. 19). Also points at 8 C were closer together than those at other temperatures. There was no significant difference between the 3 and 10 ml. treatments, their overall means being 0.331 and 0.373 percent water/hour respectively.

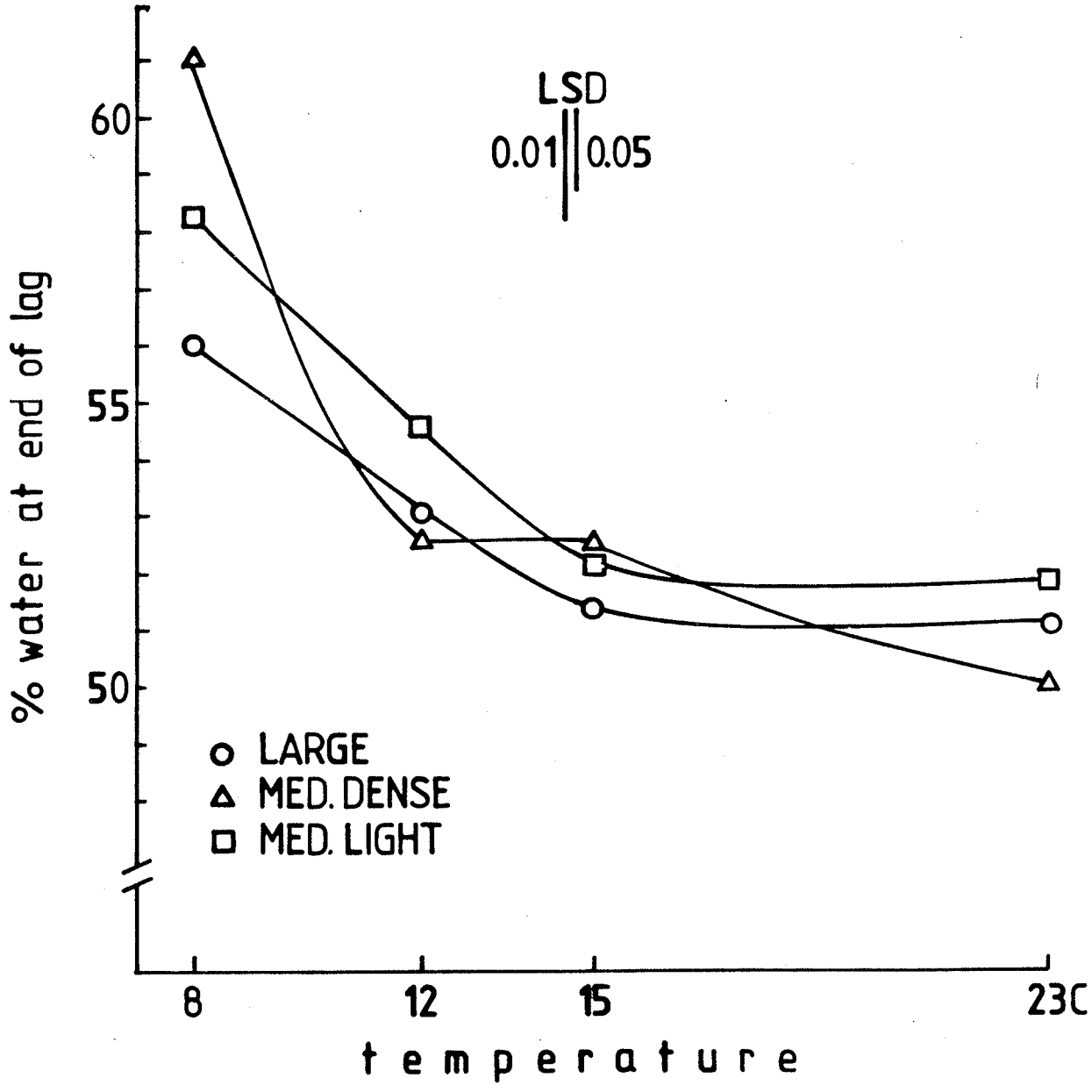


Fig. 18, Water % (d, w, basis) at the end of lag time (Neepawa). $L.S.D._{0.05} = 1.43$.

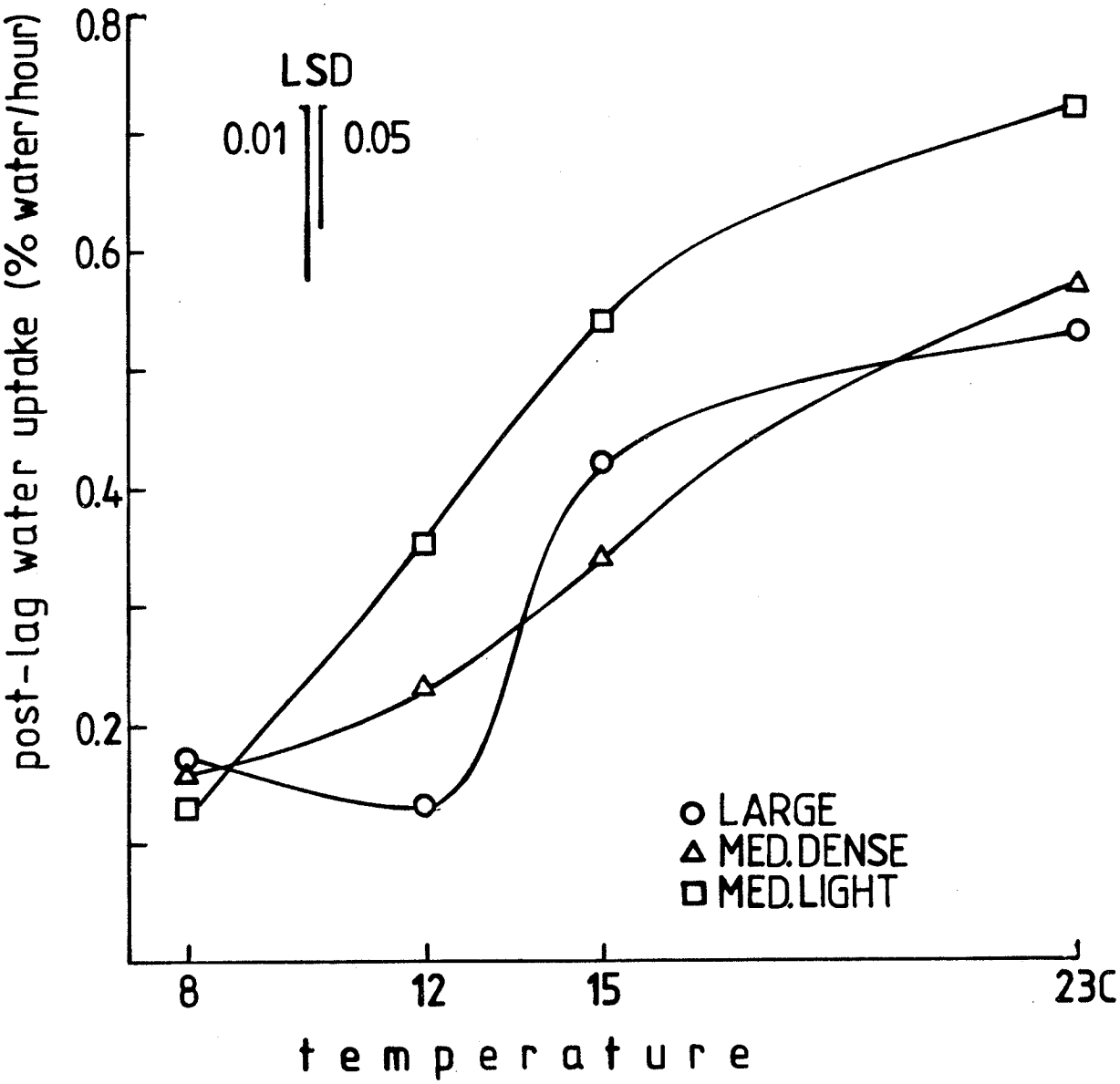


Fig. 19. Post-lag water uptake rate in % per hour (Neepawa). L.S.D.$_{0.05}$ = 0.107.

The uptake rates in Figure 19 are expressed in units of percent water (dry weight basis of 50 seeds) per hour. If actual uptake curves expressed in mls. per hour are plotted (Fig. 20), the effect of size becomes less defined.

9.3.7 Percent Water at 50% Germination (Neepawa)

Temperature and sand water appeared to be the main factors determining percent water at 50% germination (Appendix, Table 22). Higher temperatures and 3 ml. sand resulted in lower percent water values (Fig. 21). Size, which showed significance at p=0.05 but not at p=0.01, behaved in an inconsistent manner (Fig. 22). Most of the variation between sizes occurred at colder temperatures while at 23 C all sizes had identical values. This accounts for the size-temperature interaction.

9.3.8 Lag-Time (Norstar)

Increased temperature and wetter sand resulted in reduced lag times (Fig. 23). No interaction was evident between temperature and sand water (Appendix, Table 23). The greatest drop in lag time occurred as temperatures increased from 8 to 12 C. At temperatures warmer than 12 C, lag reductions were more gradual and almost linear. The 10 ml. sand water treatment resulted in about a two-hour decrease in lag time.

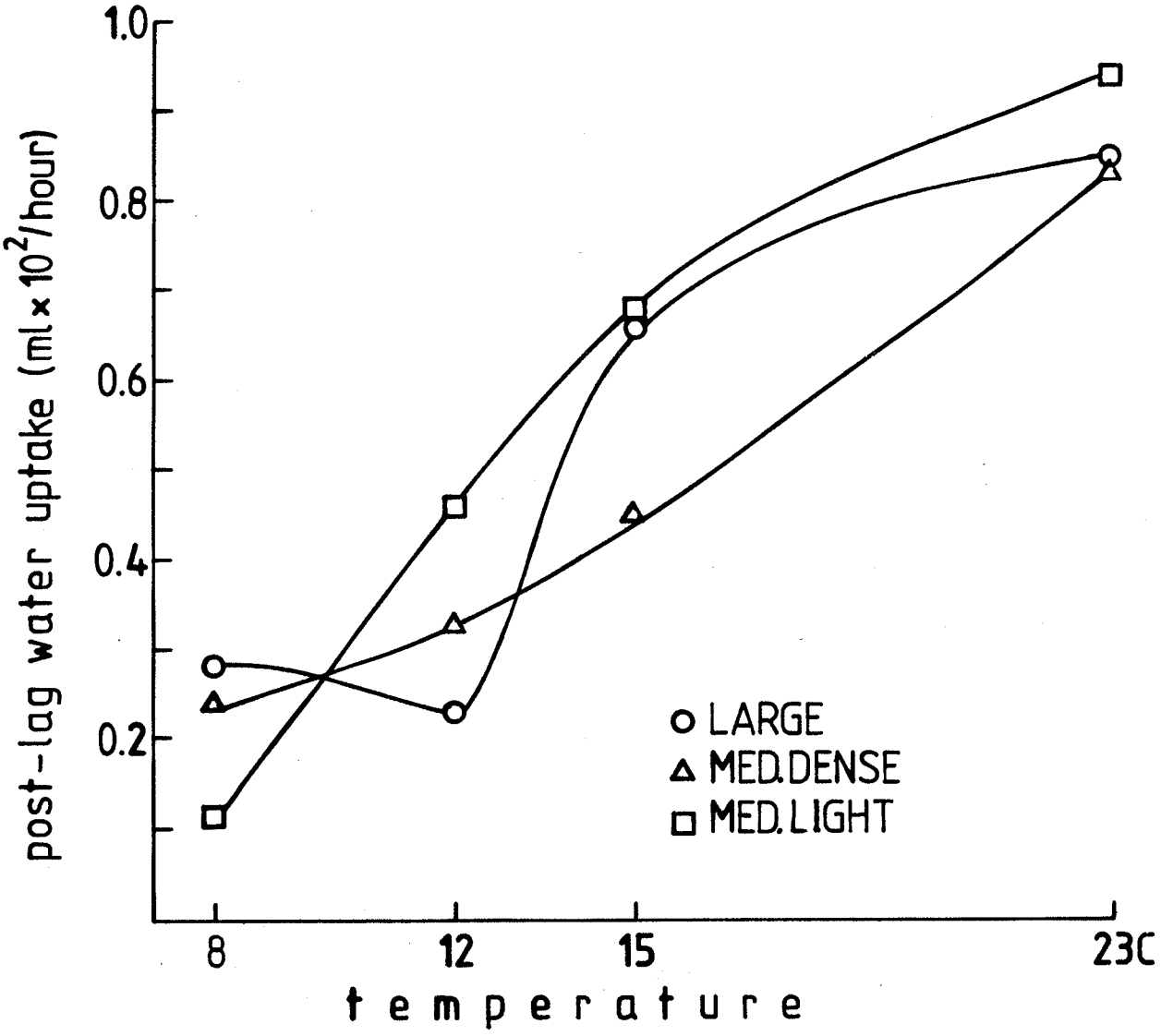


Fig. 20. Post-lag water uptake rate in ml. per hour (Neepawa).

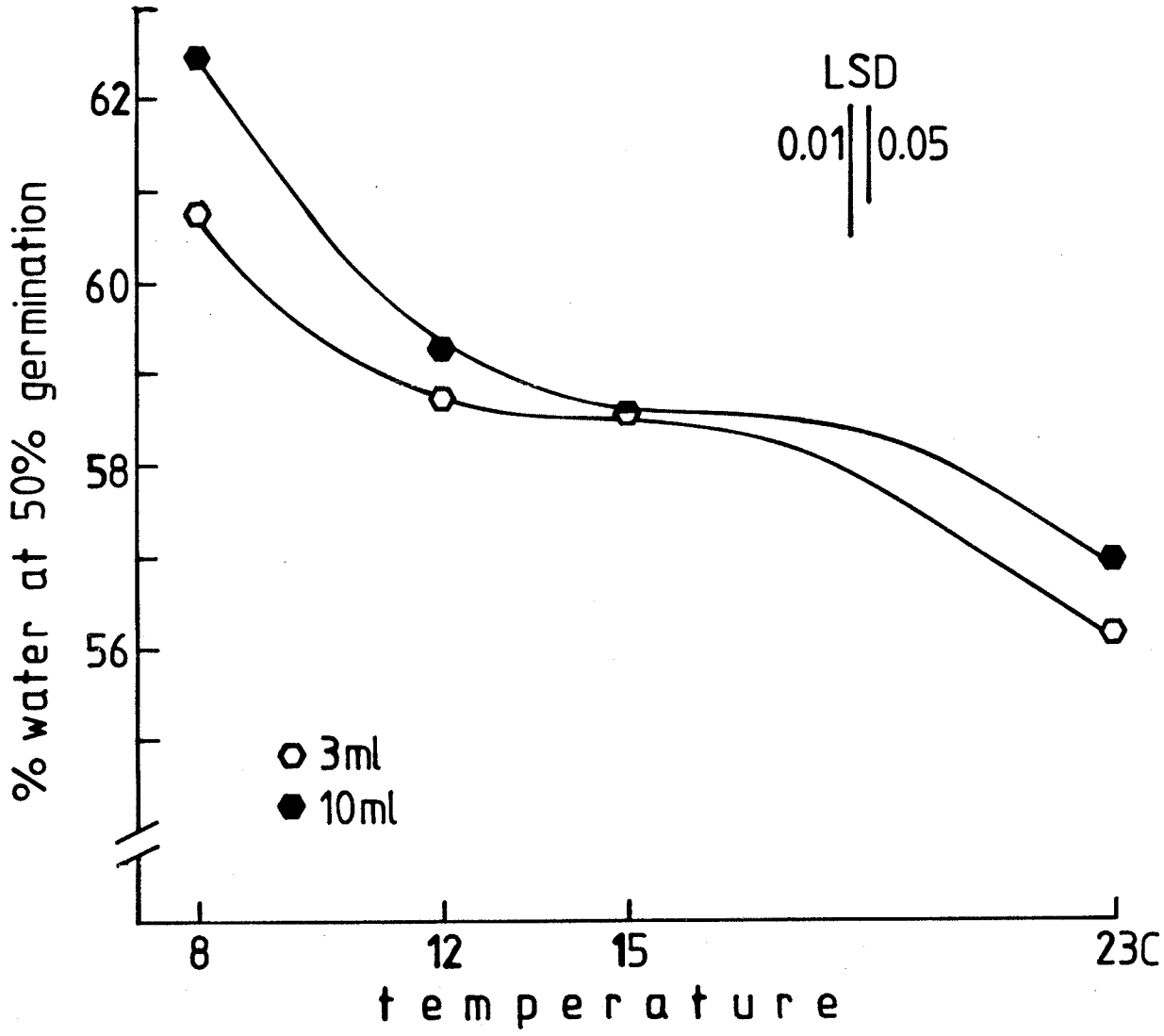


Fig. 21. Water % (d. w. basis) at 50% germination at two sand water levels (Neepawa). $L.S.D._{0.05} = 1.05$.

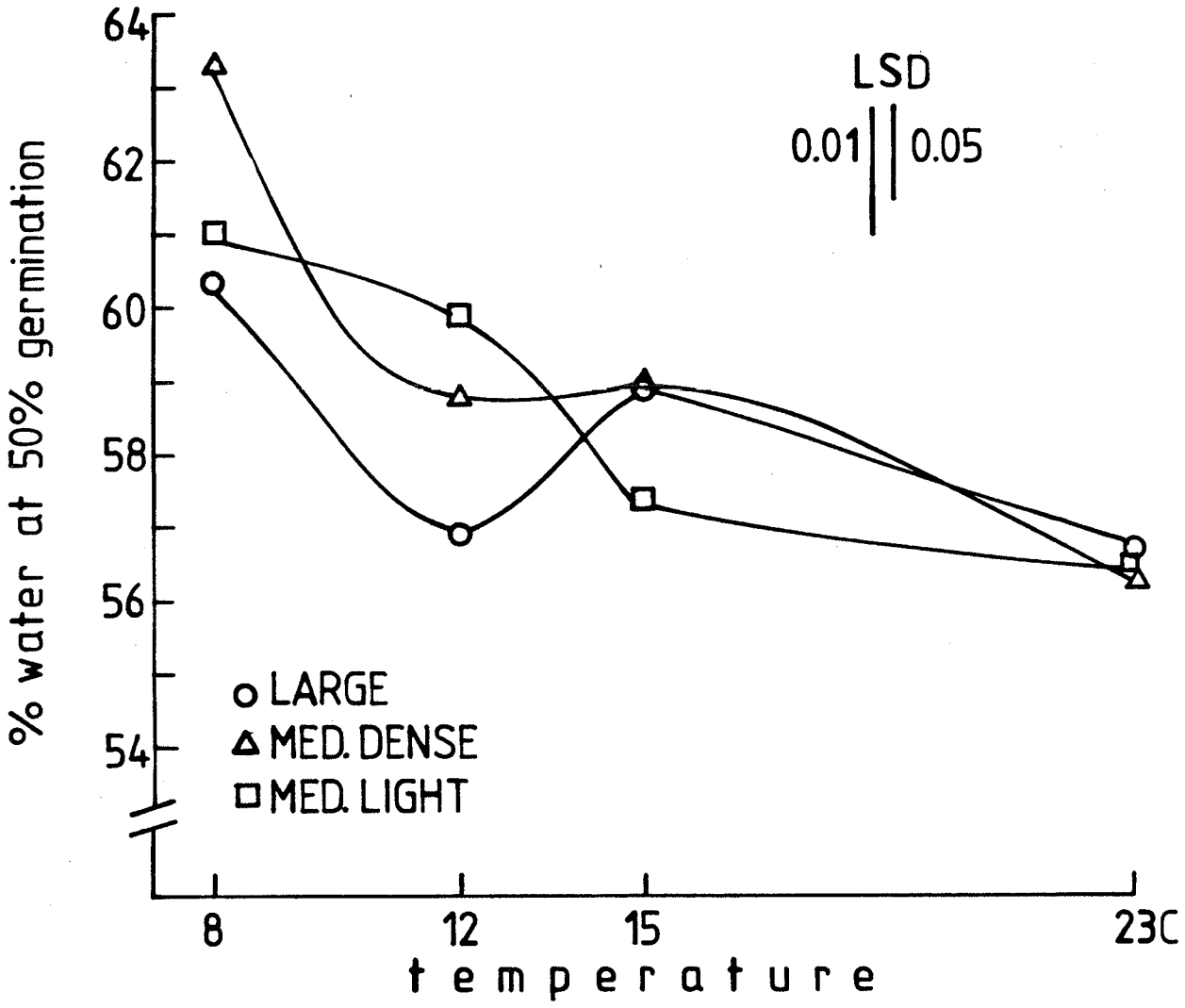


Fig. 22. Water % (d. w. bases) at 50% germination of three seed sizes (Neepawa). $L.S.D._{0.05} = 1.29$.

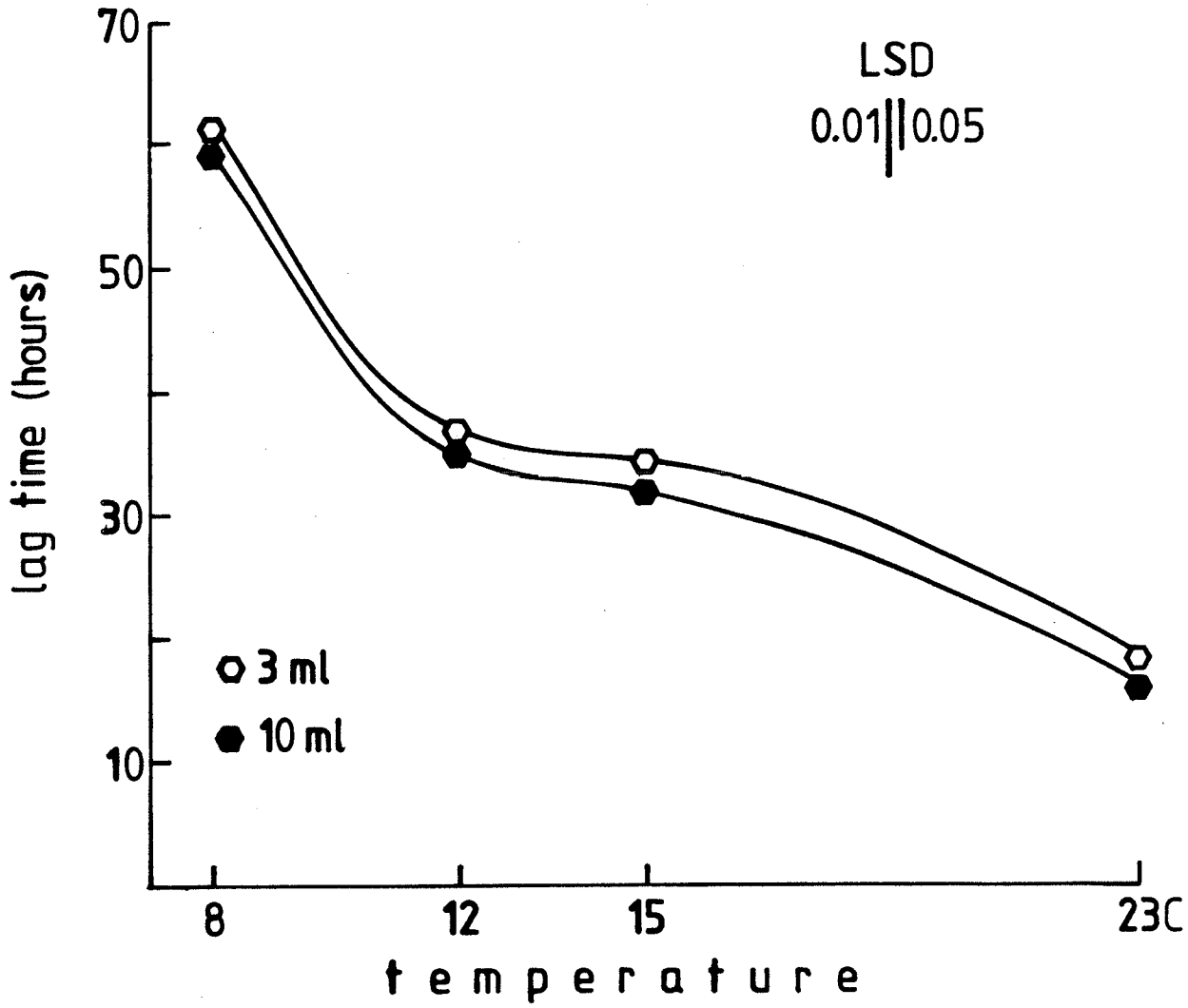


Fig. 23. Lag time (Norstar). $L.S.D._{0.05} = 4.12$.

9.3.9 Post-Lag Rate of Germination (Norstar)

The rate of germination was affected by temperature (Appendix, Table 24). At 15 and 23 C, the rate was fastest, being about 0.4 hours/seed whereas the 8 and 12 C treatments resulted in rates of about 0.6 hours/seed (see Fig. 24). There was a sharp drop in the rate as temperatures decreased from 15 to 12 C. Although there was no significant difference between the two water treatments, the 3 ml. treatments always had a faster mean rate than the 10 ml. treatments.

9.3.10 Hours to 50% Germination (Norstar)

Both temperature and sand water affected time to 50% germination (Appendix, Table 25). There was a fairly linear increase in delay to 50% germination as temperatures decreased from 23 to 12 C. A further reduction to 8 C resulted in an increased rate of delay in hours (see Fig. 25). Seed germinated in 10 ml. sand generally reached 50% germination slightly over an hour sooner than their 3 ml. counterparts.

9.3.11 Percent water at end of lag (Norstar)

Temperature and sand water significantly affected percent water at the end of lag time at $p=0.05$. Only temperature was significant at $p=0.01$. No interactions were present (Appendix, Table 26). Water content at the end of the lag period varied from a low of about 37% to a high of

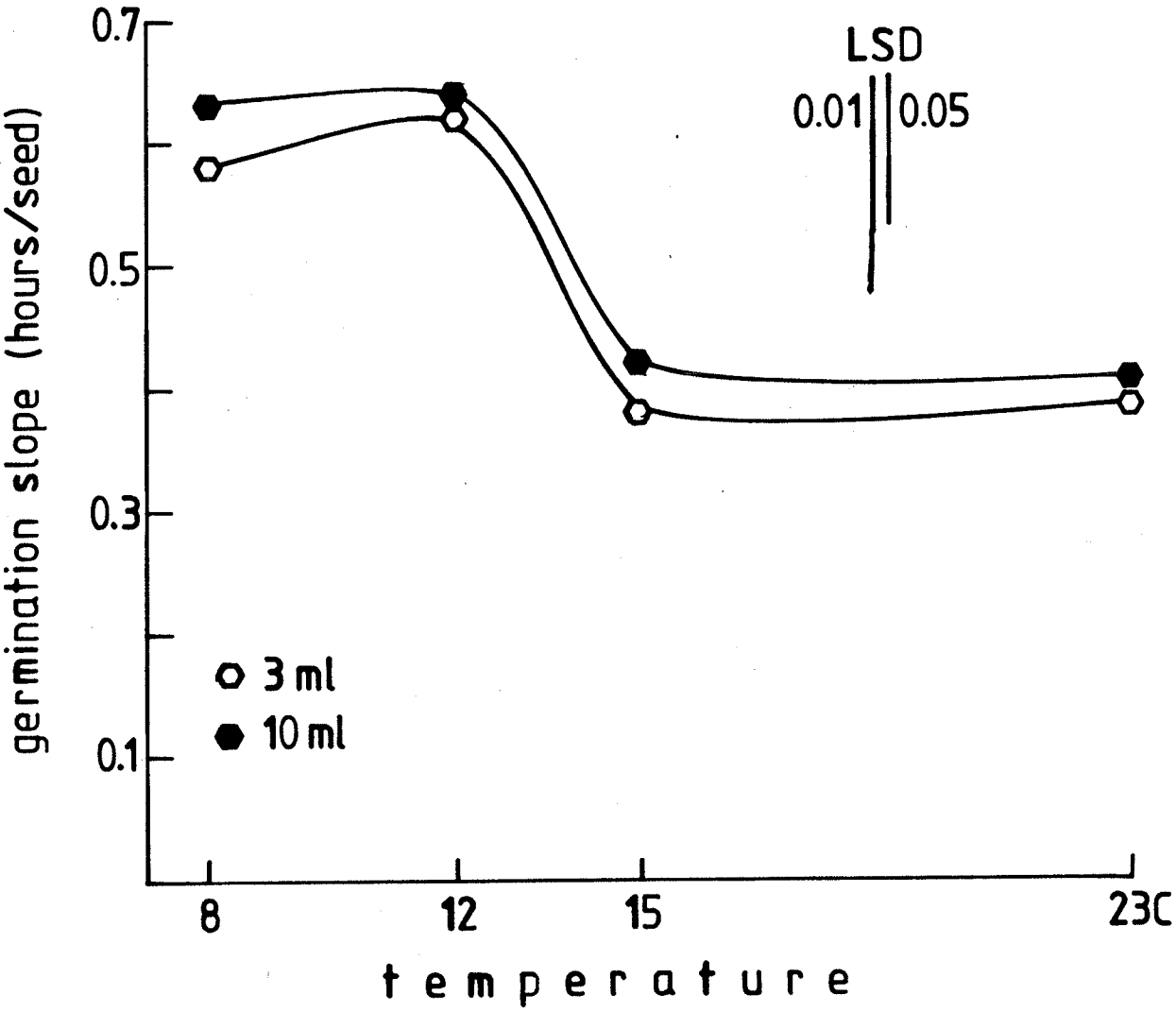


Fig. 24. Germination rate (Norstar). $L.S.D._{0.05} = 0.121$.

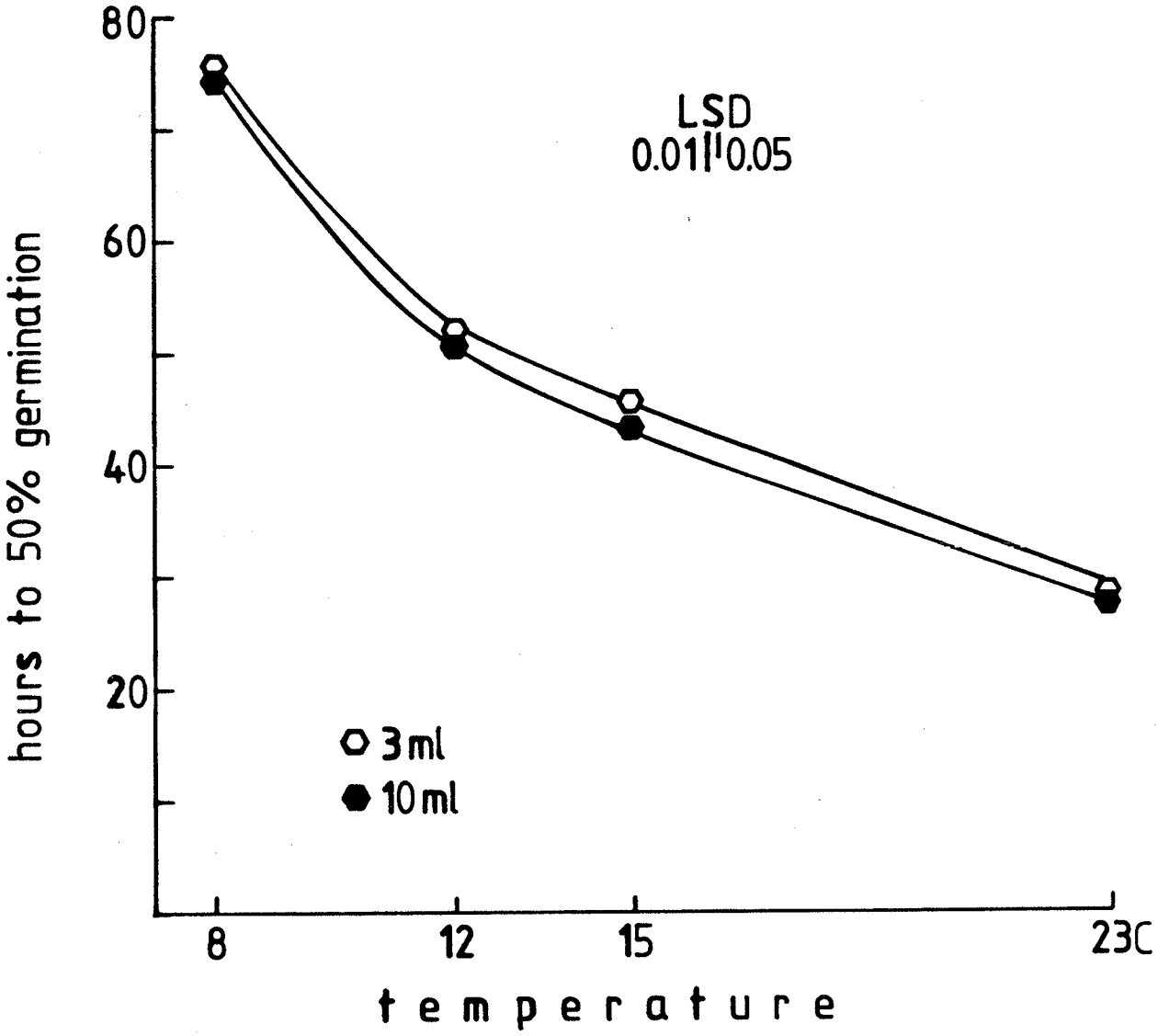


Fig. 25. Hours to 50% germination (Norstar). $L.S.D._{0.05} = 2.09$.

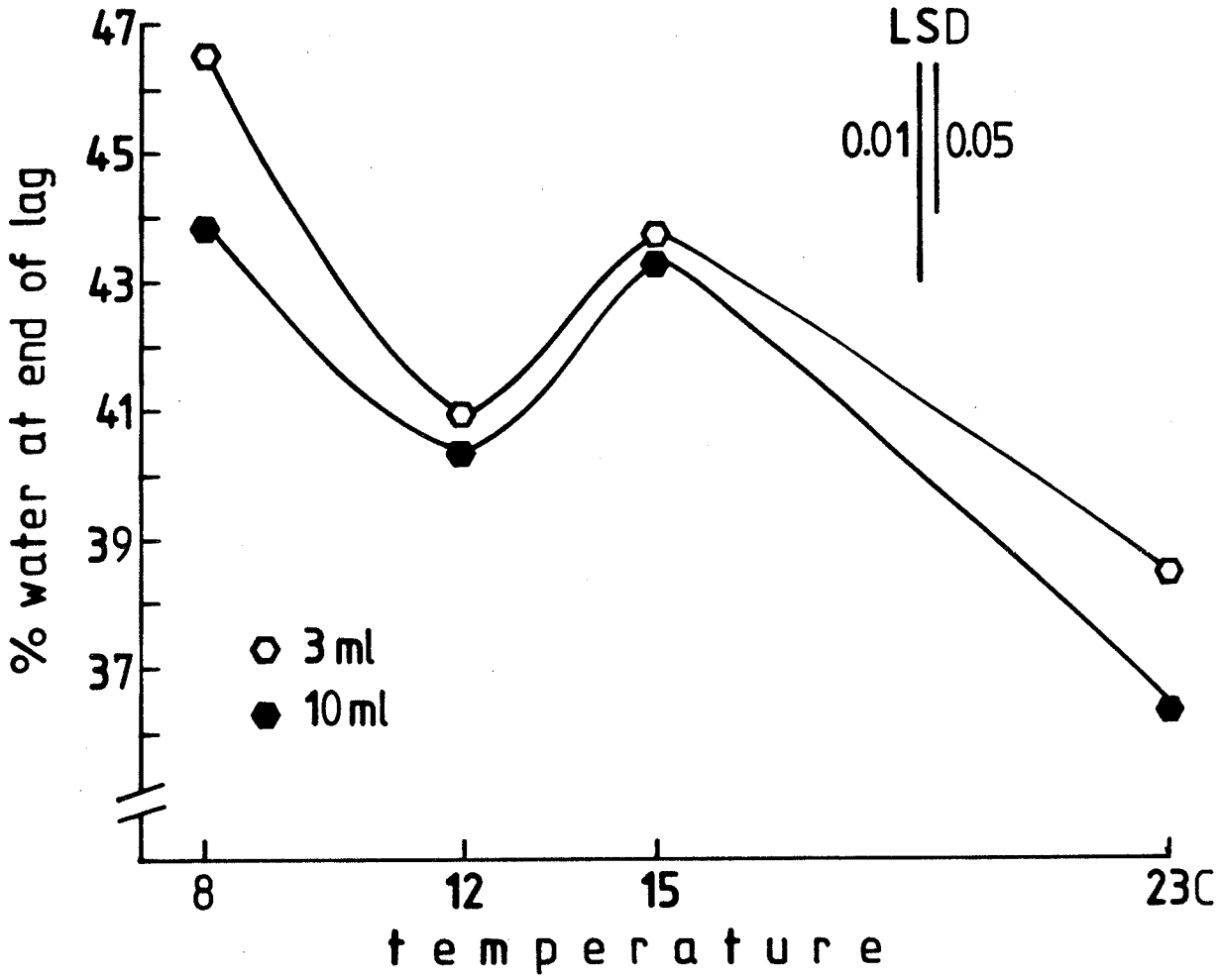


Fig. 26. Water % (d. w. basis) at the end of lag time (Norstar). L.S.D.$_{0.05}$ = 2.37.

46% (Fig. 26). Even though irregular behaviour occurred at 12 and 15 C, it appeared as if increased temperature decreased the water content at the end of the lag period. Similarly, seed germinated on wet sand always had a lower percent water than those on the drier sand.

9.3.12 Post Lag Water Uptake Slope (Norstar)

Only temperature affected the post-lag water uptake rate (Appendix, Table 27). At temperatures from 8 to 15 C water uptake rate seemed to be fairly uniform: about 0.25% per hour (dry weight seed basis). At 23 C however, the rate approximately doubled (Fig. 27). Even though no significant differences were evident with respect to sand water, the 10 ml. treatments consistently had a somewhat higher mean uptake rate.

9.3.13 Percent water at 50% germination (Norstar)

Temperature significantly affected percent water at 50% germination (Appendix, Table 28). Seed water content at time of 50% germination decreased with increased temperature (Fig. 28). A slight deviation to this rate occurred at 12 and 15 C. No significance was found between water treatments, although the 10 ml. treatments always were slightly lower than the 3 ml. ones.

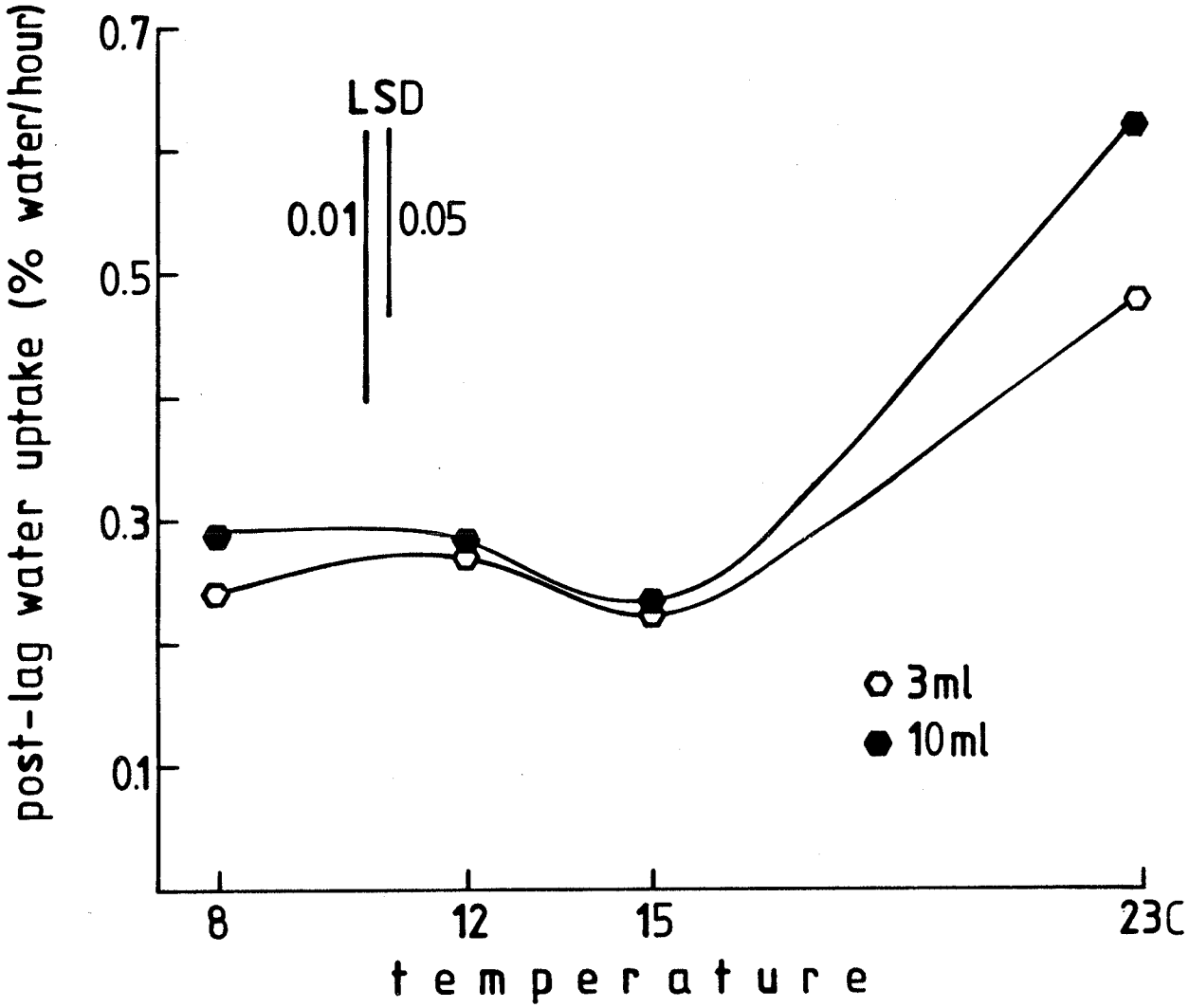


Fig. 27. Post-lag water uptake rate (Norstar). $L.S.D._{0.05} = 0.149$.

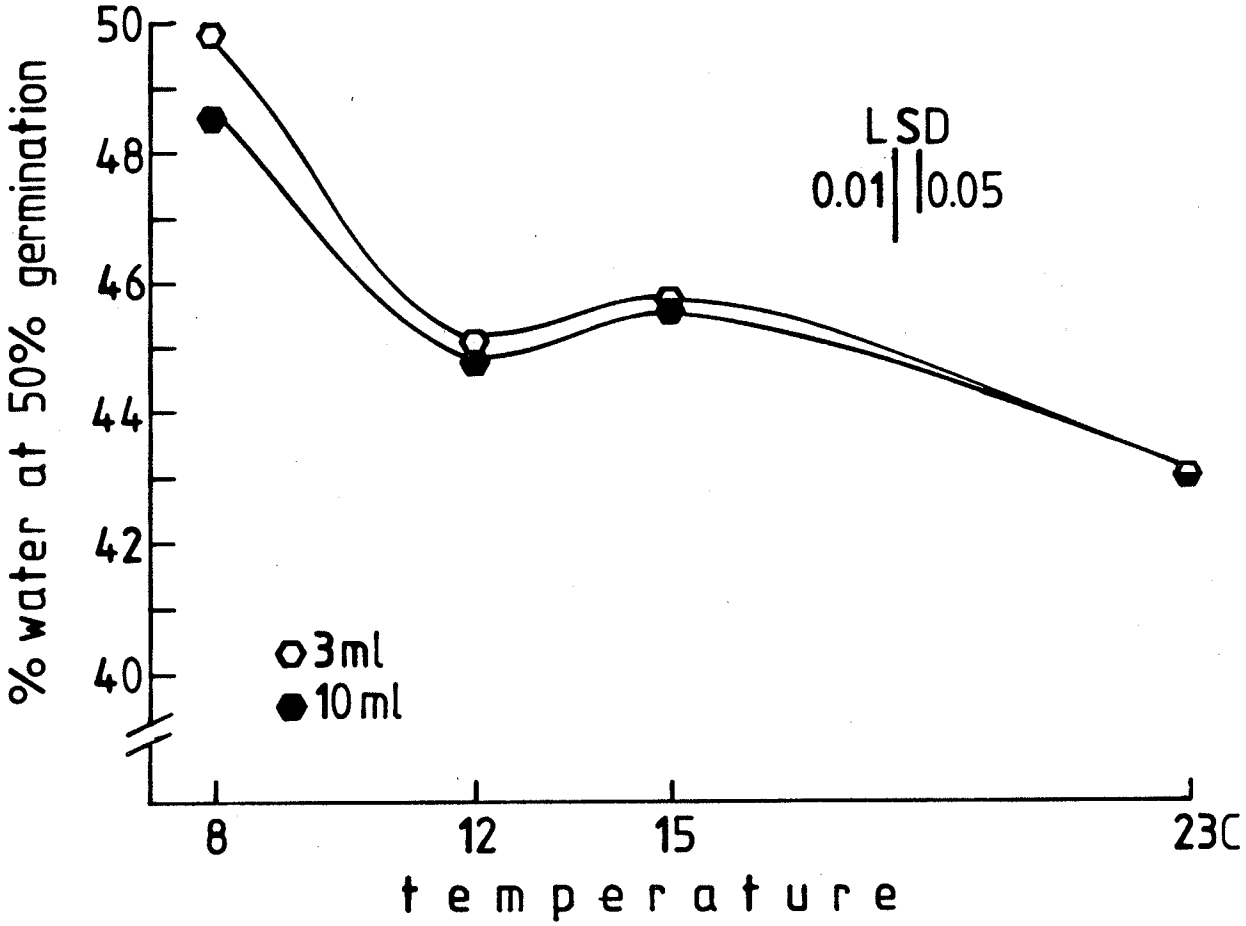


Fig. 28. Water % (d. w. basis) at 50% germination (Norstar).
$L.S.D._{0.05} = 1.00$.

9.3.14 Discussion

The effect of the Neepawa seed sizes (Part A) appeared to constantly only affect lag time and hours to 50% germination, with higher values associated with larger seeds. The other four dependent variables were not at all, or only inconsistently affected by size. Higher water requirements of larger seeds delay germination (Muchena and Grogan, 1977). Some of the inconsistencies associated with the fraction size variable might have been due to density. Kernel hardness was determined to be different between the medium light and dense fractions, with the dense fractions being harder. The pearling resistance value which represents material remaining (pearls) in grams from 20 gm. samples for 20 sec., were 9.2 and 10.1 g., respectively for medium light and medium dense seed in four replicates, a difference significant at $p=0.01$. The degree of hardness would influence water uptake and movement (Campbell and Jones, 1955).

Since temperature and sand water effects were examined for both Neepawa and Norstar wheats, a discussion which compares the two wheats with these factors is included. Precise comparisons between the Neepawa and Norstar results are not entirely possible given that the medium seed size of the Norstar did not correspond entirely with any of the Neepawa fractions. Nevertheless, general comparisons reveal considerable differences between the wheats.

In all cases, increased temperatures resulted in decreased lag and 50% germination times (Fig. 29). The post-lag rate of germination was greater at the two warmer temperatures than at the two colder temperatures. This is represented by smaller slopes in Fig. 29. The Norstar wheat had a shorter lag and hence shorter time to 50% germination, especially at colder temperatures. The post-lag germination rates were similar in both wheats at a given temperature.

Lag time played a much more important role in determining hours to 50% germination than the post-lag germination rate. Its value ranged from 63% in warmer to 80% in colder conditions, of total time to 50% germination. This would indicate that the delays associated with cold temperature are largely the result of increased lag time, a finding consistent with the results of Blackshaw et al. (1981) and Hallam (1981).

The water content at the end of the lag period and at 50% germination increased with decreased temperatures (Fig. 30). In this figure the results of the three Neepawa sizes were combined as they were similar. Blacklow (1972), using corn, noticed higher water contents at colder temperatures also. This is probably related to more water being bound and slower movement (Mohsenin, 1970). Since seeds gained similar amounts of water between the end of lag and 50% germination at all temperatures, temperature effects were caused during the lag period. By the end of the lag

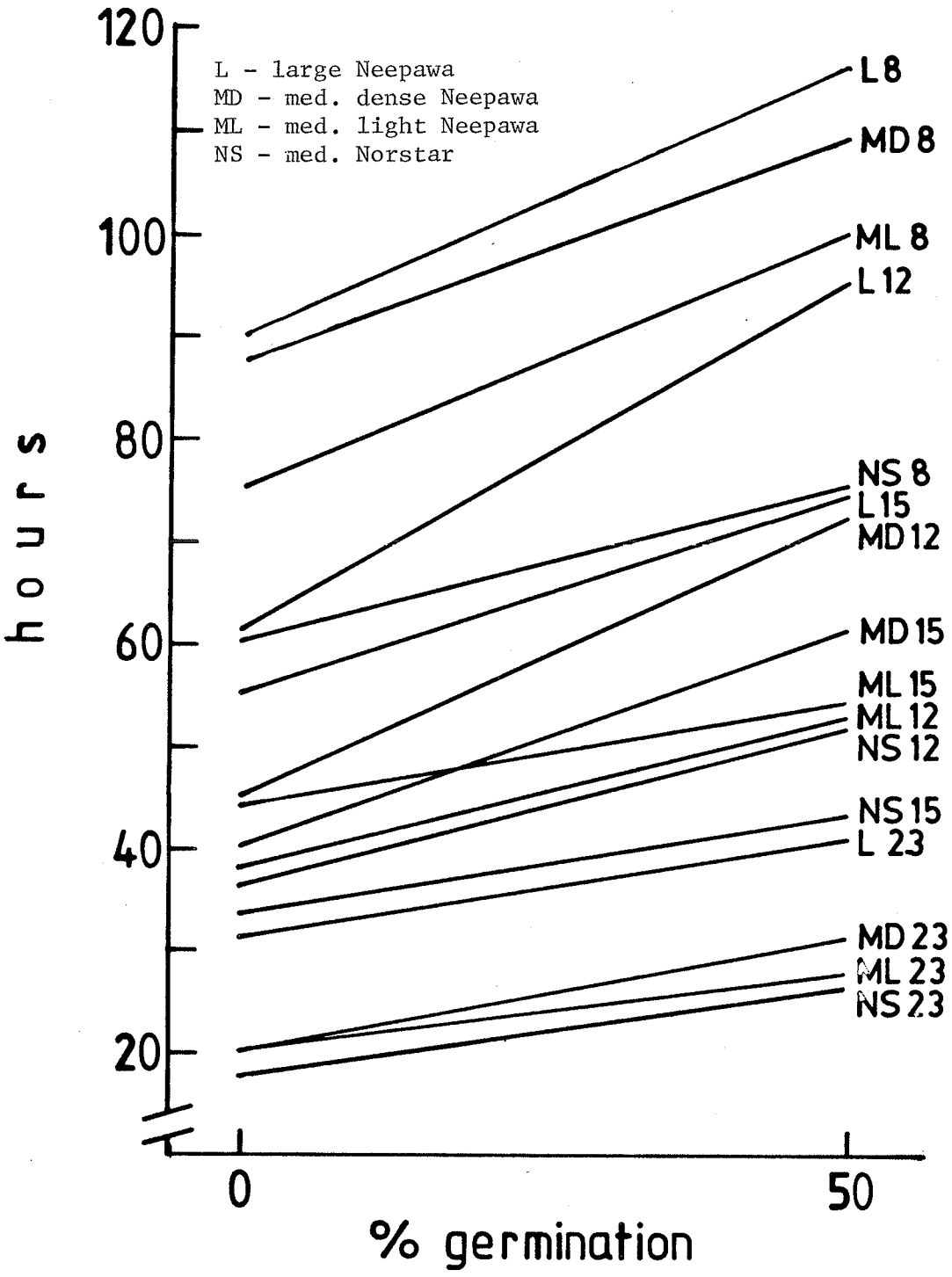


Fig. 29. Lag time, rate of germination, and hours to 50% germination of Neepawa (three sizes) and Norstar (one size) wheats at four temperatures.

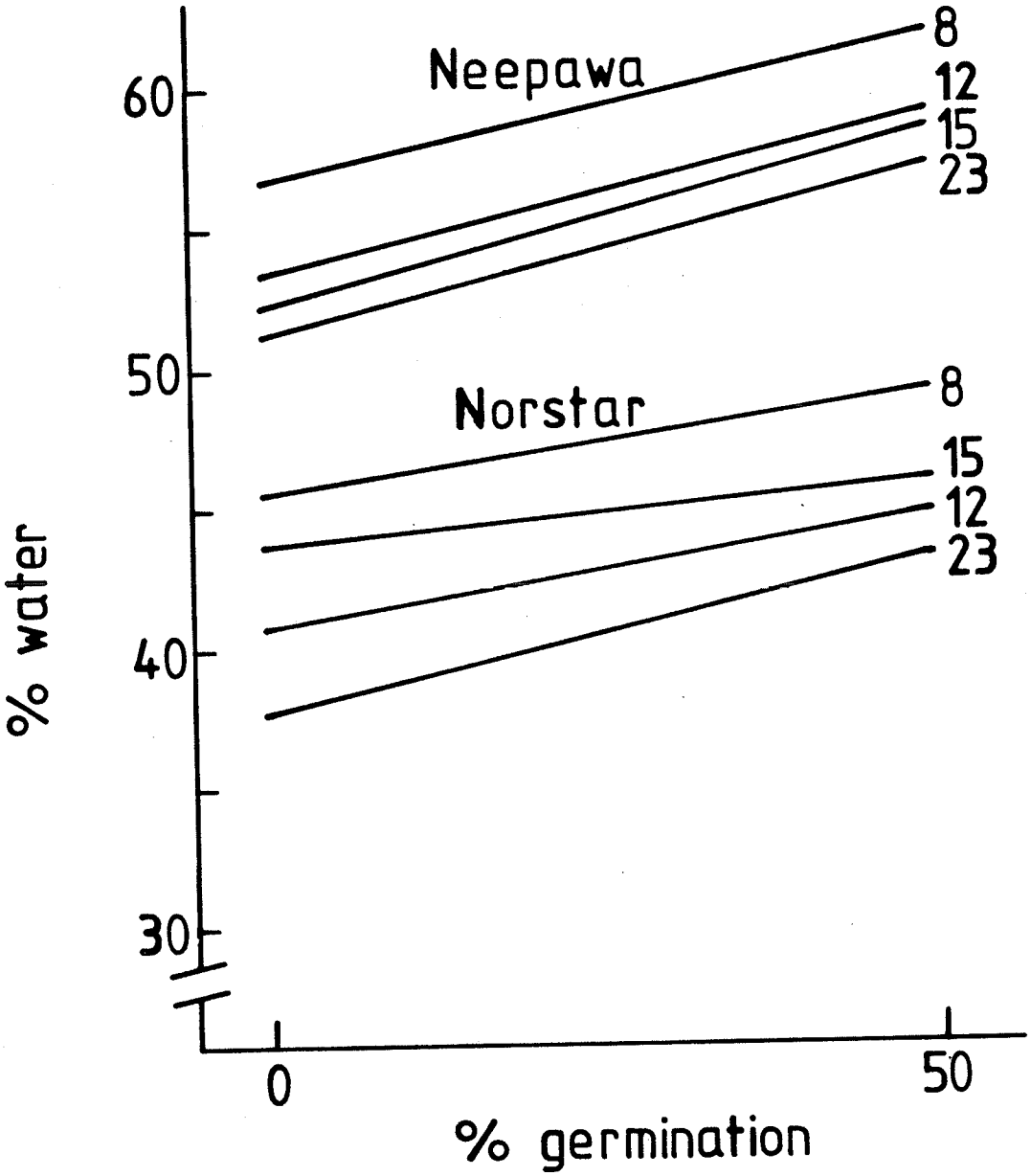


Fig. 30. Water % (d. w, basis) at lag time and 50% germination of Neepawa (average of three sizes) and Norstar wheat at four temperatures.

time, seeds had reached between 87% and 95% of the water content reached at 50% germination. Water uptake rates during germination, when expressed in percent gain per hour (and not in percent gain per seed germinated as shown in Fig. 30) were slower at colder temperatures but were accompanied by a longer duration in germination. The Norstar wheat had lower water requirements for germination. At both the end of lag and at 50% germination, its percent water values were 70 to 80% those of the Neepawa at a given temperature. It is not known whether this was just a variety or seed lot effect, possibly due to different protein levels, or if it involved behavioral differences associated with spring and winter wheats.

Differences arising from the two sand water levels were not as strong as those of temperature, but nonetheless showed interesting trends. With 10 ml. water in the sand, both the end of lag and 50% germination occurred significantly sooner in both wheats (at $p=0.05$). No significant difference in the post-lag germination rate was observed. Although not always significant, the 10 ml. treatments resulted in somewhat higher water contents at both the end of lag and 50% germination. Since increased sand water had a stronger effect on reducing hours rather than increasing seed water content at germination, this would suggest that the sand's hydraulic conductivity was more limiting than that of the seed. In other words, higher sand hydraulic

conductivity associated with increased sand water content reduced hours more than it increased seed water content. This is in agreement with density studies (Experiment 3; Shaykewich and Williams, 1971b) in which lower seeding density resulted in a less rapid decline in soil hydraulic conductivity and hence more rapid germination.

Chapter X

EXPERIMENT VII - VAPOUR PHASE WATER UPTAKE EXPERIMENTS

10.1 INTRODUCTION

Vapour phase water uptake experiments were conducted by placing seeds above a liquid pool of water. In this manner, the water could only reach the seed via the vapour phase, thereby causing water uptake to be slower and more controlled. Owen (1952) used vapour phase uptake to allow wheat to germinate at various water potentials. In this study, seed water contents and germination (if it occurred) were measured at regular intervals using only pure water (0 water potential) at various temperatures.

10.2 MATERIALS AND METHODS

One pint (568 ml.) GEM canning jars (8 cm. diameter x 10 cm. height) were used as the vapour uptake chambers in the experiment. Seeds were suspended in cages made of aluminum window screening having 1.67 mm. square openings (see Figure 31). Aluminum window screening was used instead of nylon window screening, since the aluminum could be shaped into rigid cages. Each cage had a flat round base 5 cm. in

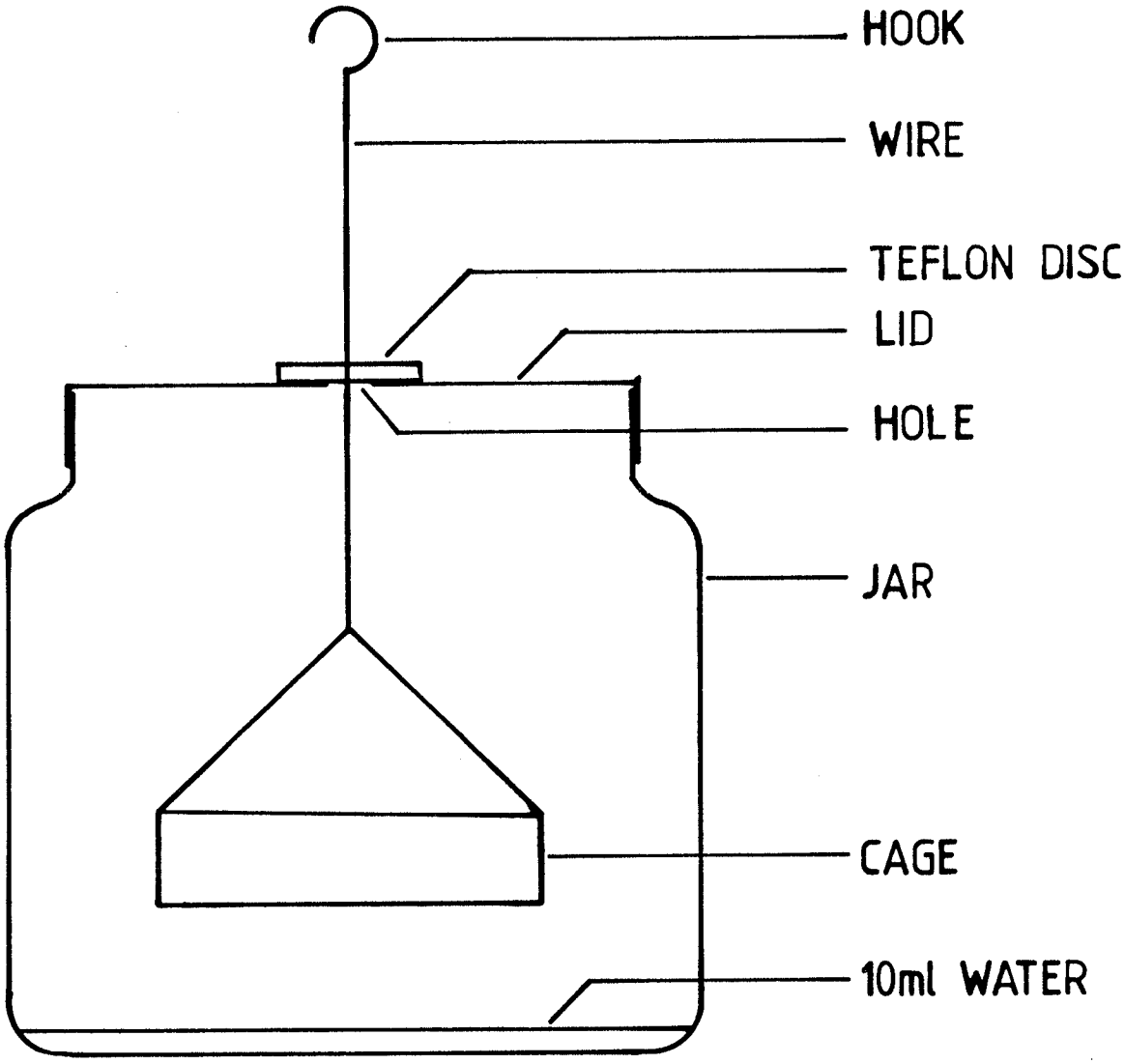


Fig. 31. Apparatus used in vapour uptake experiments.

diameter with a 1 cm. wall around the edge. The cage was attached to a 12 cm. long brass wire which passed through a 4 mm. diameter hole at the centre of the metal lid of the jar. Above the hole in the lid, the wire was pushed through the centre of a teflon disc (1.5 cm. diameter x 0.2 cm. thick). This disc served two purposes. It kept the wire cage assembly at the proper height since the friction between the disc and the wire was sufficient to support the cage assembly filled with seeds. The disc also sealed the jar preventing vapour exchange between the interior and exterior of the jar. The end of the brass wire was bent into a hook. This hook allowed the whole wire-cage assembly to be weighed without opening the jar and disturbing the seed. During weighing, the whole assembly was lifted slightly, so that the teflon disc no longer rested on the lid. Care had to be taken to ensure that neither the wire touched the edge of the lid, or that the cage touched the side of the jar, thereby preventing erroneous weight values. Predetermined weight values included the empty cage assembly, and also the cage filled with air dry seed (11% water) at the beginning of the experiment. With this information, it was easy to calculate the percent water (d.w. basis) in subsequent readings.

Since the vapour pressure of water is temperature dependent, it was important to maintain uniform temperatures. Small shifts in temperataure would cause water vap-

our to condense on the seeds or the lid resulting in erroneous weighings. Jars were placed in temperature controlled water baths (< +/-0.5 C). In order to keep the jars from floating about in the water bath, or rocking back and forth due to the presence of rapid water flow from water circulation, the jars were tightly secured to the base of the water bath using thick elastic bands stretched over the tops of the lids. The result was that the jars, even though they were 90% submerged in water, were immobile, yet could easily be removed, weighed, and replaced in a matter of seconds. Since the top of the lids were not surrounded by water, insulation placed over the water bath minimized the influence of lab temperatures.

Unless otherwise specified, the distance between the bottom of the cage and the water surface was 2.7 cm. Jars contained 10 ml. water at the start of the experiment; much more than required for all 50 seeds in the cage.

The cages were weighed regularly for the duration of the experiment, which depended on temperature and condition of the seeds.

Preliminary experiments demonstrated that under cold temperatures in which uptake was slow, seeds were prone to begin rotting after long periods. In order to minimize this problem, seeds were lightly dusted by a talc-fungicide mixture prior to the start of the experiment. Talc was included so that the concentration of fungicide would not be un-

reasonably high, and was used at rates of 9 parts talc to 1 part fungicide. The fungicide used was panogen. A preliminary test comparing dusted and control seeds displayed no difference in the rate of vapour uptake.

For each temperature, control cages were set up without seeds in them. Generally the weight of the cages remained constant throughout the duration of the experiment. In a few cases, very minor changes in weight were observed, but they probably were due more to variations in weighing. No cage oxidation or water condensation was observed.

10.3 VAPOUR PHASE EXPERIMENT

10.3.1 A: The effect of distance from liquid water to the seed cage

A study was conducted to determine what effect the distance of the gap between the liquid water and the suspended seeds had on the water uptake rate. Fifty large Neepawa seeds placed in the screen cages were suspended at three different heights - 3, 18, and 32 mm. The jars were placed in 23 C conditions. Two replicates were used in this completely randomized experiment.

10.3.2 B: Effect of seeding density in cage - Competition for Water Vapour

A study was conducted to determine the effect of seeding density on water uptake. Either 50 or 25 medium

dense Neepawa seeds were placed in the standard 50 mm. diameter screened cage as described with a 2.7 cm. gap between water and cage. The containers were in 23 C temperatures. Water uptake and percent water was calculated periodically. This completely randomized design had five regular (50 seed) and two low (25 seed) replicates.

10.3.3 C: Effect of Temperature, seed size, and wheat variety on vapour uptake and germination

A study was conducted to determine the effects of temperature, seed size, and wheat variety on vapour uptake and germination. The gap between water and the cage was 27 mm. The sixteen various treatments are shown in Table 2. Percent water and germination values were regularly determined.

Although only two replicates are usually reported for all treatments, normally a total of four to eight jars were set up for each treatment, half for each replicate; not all at the same time. By having staggered starting times, it was possible to get many more points on the curve. Containers were weighed regularly throughout the duration of an experiment, so that a set of containers started at a given time did not dominate the curve in any region.

Seeds were weighed very regularly at the beginning of experiments, usually every 4 to 6 hours per jar for two days, as uptake during this time was rapid. Once uptake levelled off, weighing was less frequent. In 10 C treatments,

TABLE 2

Vapour Phase Uptake Treatments

Temperature	Seed	Size
10 C.	Neepawa	medium-light
	Neepawa	mediuim-dense
	Neepawa	large
	Norstar	medium
15 C.	Neepawa	medium-light
	Neepawa	medium-dense
	Norstar	medium
20 C.	Neepawa	medium-light
	Neepawa	medium-dense
	Norstar	medium
23 C.	Neepawa	medium-dense
	Neepawa	large
	Norstar	medium
25 C.	Neepawa	medium-dense
	Neepawa	large
	Norstar	medium

for example, where runs lasted for well over three weeks, the last several days had weighings reduced to about one per day per jar, since weight changes were very small. Consequently, the plotted curves of combined jars per replicate had points very close together initially, but further apart later on.

10.4 RESULTS AND DISCUSSION

10.4.1 A: Effect of distance from liquid water to seed

Distance significantly affected the rate of water uptake by seeds. By 24 hours, seeds which were 3 mm. from the liquid water had reached a mean 33% water whereas those at 32 mm. were only at 23% (see Fig. 32a). After that, the uptake slopes became fairly equal, with the 3mm. treatment remaining approximately 10% above the 32 mm. counterpart. When uptake rates instead of values were plotted (Fig. 32b), unexpected 17.5 and 32 mm. curves resulted. The fairly sizable L.S.D. values suggest that the predicted means are on the wrong location as there should be separation between the two curves if distance indeed has an effect. Owen (1952), did not notice a distance effect, whereas Collis-George and Melville (1978) did.

Since the danger of accidently spilling liquid water on the seeds during weighing was greatest with the small gaps, a wider gap of 27 mm. was used in determining water uptake in all other vapour phase uptake experiments.

10.4.2 B: Seeding Density in Cage

The higher seeding density (50 seeds/cage) resulted in a slower more gradual water uptake compared to the low density treatment (25 seeds/cage). Up to 100 hours the low density seeds had a mean water percent of 1 to 3% higher than the 50 seed treatment. After 100 hours the curves

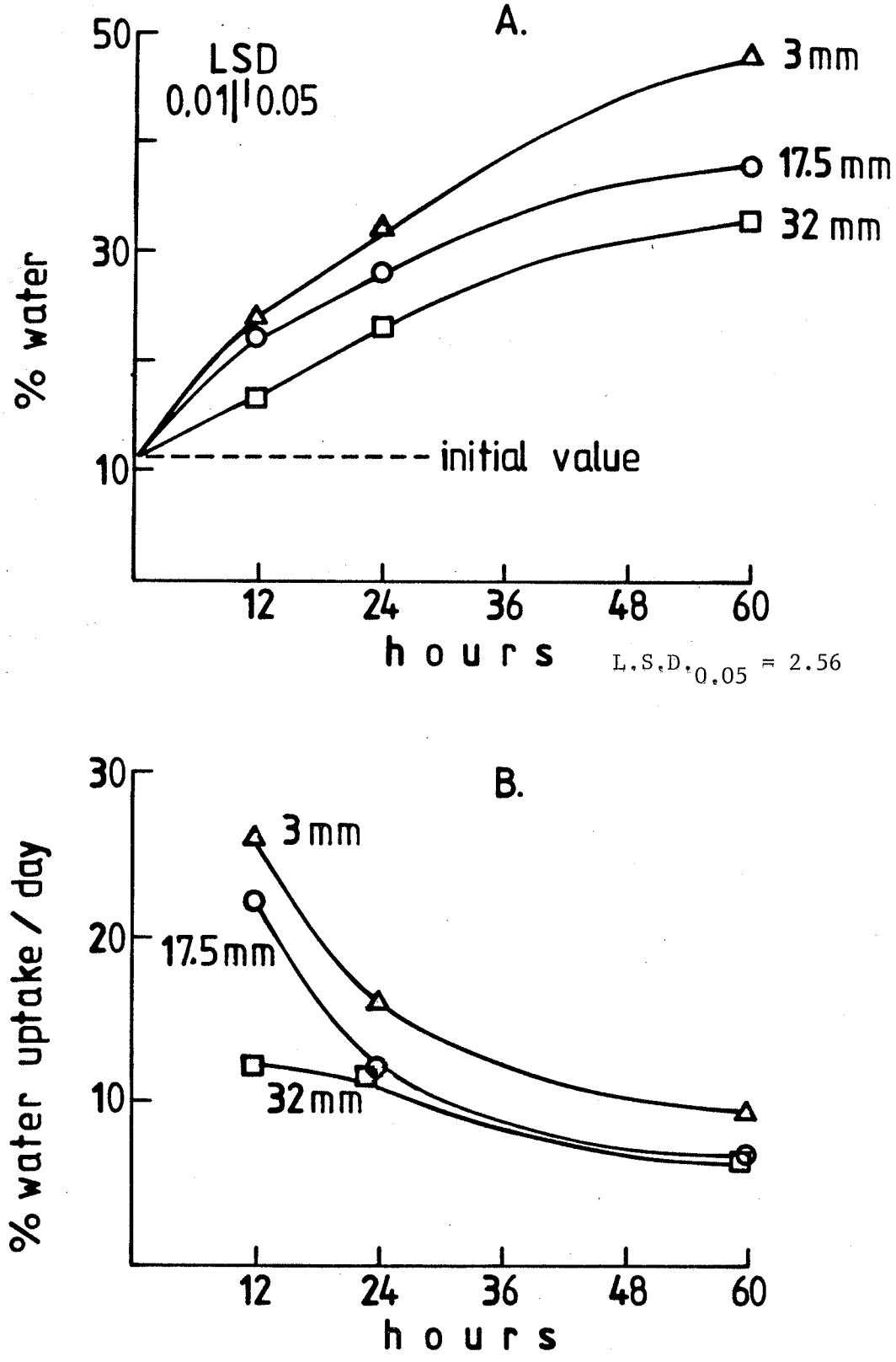


Fig. 32. Effect of cage distance from water; A.) water % (d. w. basis) with time, B.) rate of wter uptake per day.

moved closer together. Although the L.S.D. values in Fig. 33 would suggest no difference between the two densities at any given time, a strong significance was evident in the overall analysis (Appendix, Table 29). Because of the strong water potential gradient between the water and the seed at low seed water contents, vapour transfer appeared to be a limiting factor. The 50 seed treatment being a larger sink did not take up water as rapidly per seed due to the limiting vapour transfer although total uptake was greater. GLM predicted percent water at any time with formulas shown in Fig. 33.

10.4.3 C: Temperature and Seed Type Effects on Water Uptake

Water content values at all the different sampling hours were analysed using GLM for all the treatments. A regression equation which fitted the data quite well was determined to be: percent water=intercept + A hours + B $\sqrt{\text{hours}}$. The R-square values for the best fitting curve as well as the intercept, A and B values for each treatment equation are given in Table 3. The R-square values for treatments 15 C and warmer were good, whereas those at 10 C were relatively low. The residuals for these 10 C treatments did not have much of a pattern, suggesting that the equations were not at fault.

The predicted curves for each treatment are shown in Figures 34 to 37. When these curves were superimposed on the actual mean values (not shown), they fit very well.

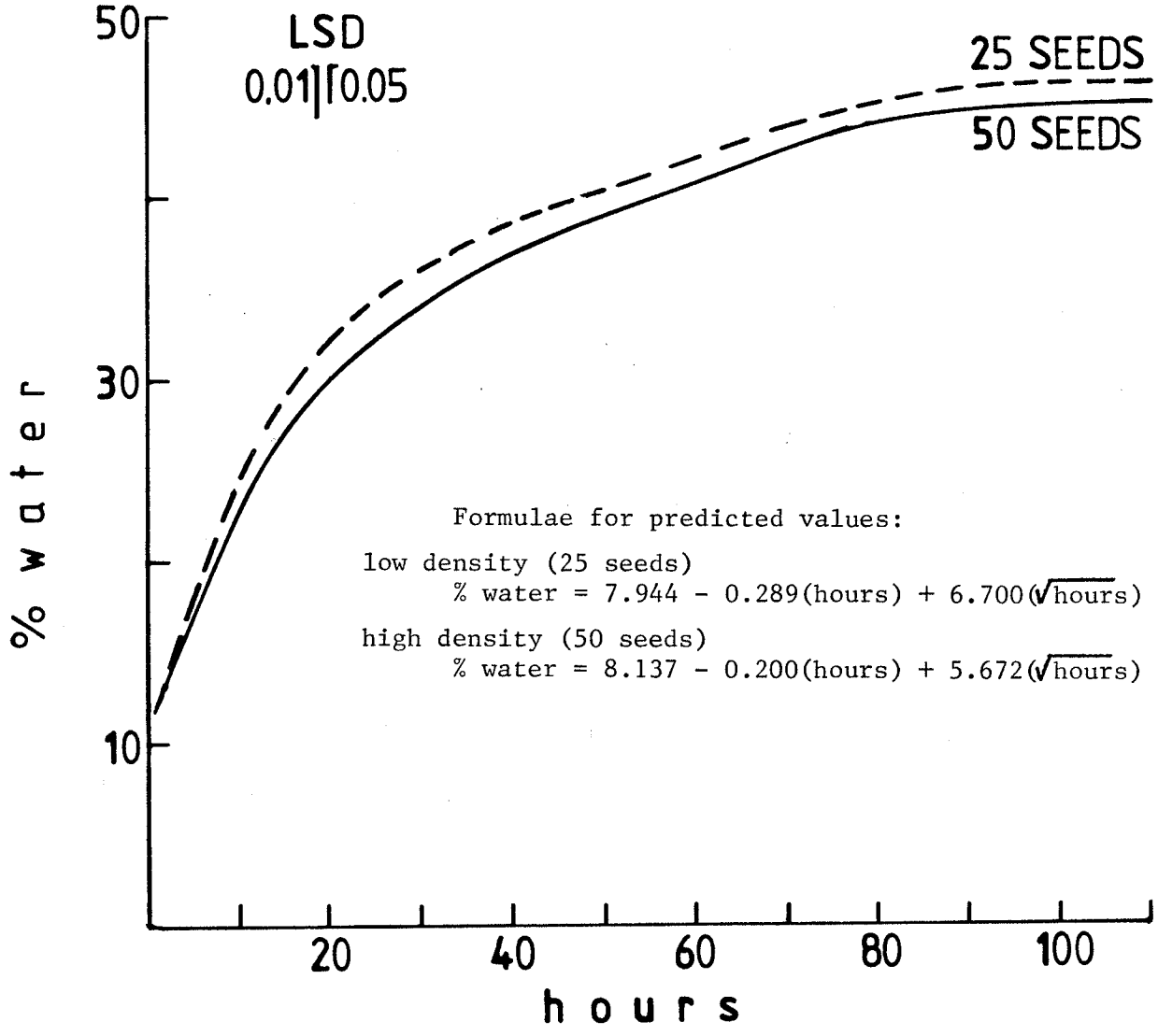


Fig. 33. Effect of seed number per cage on vapour upake (% water d. w. basis).

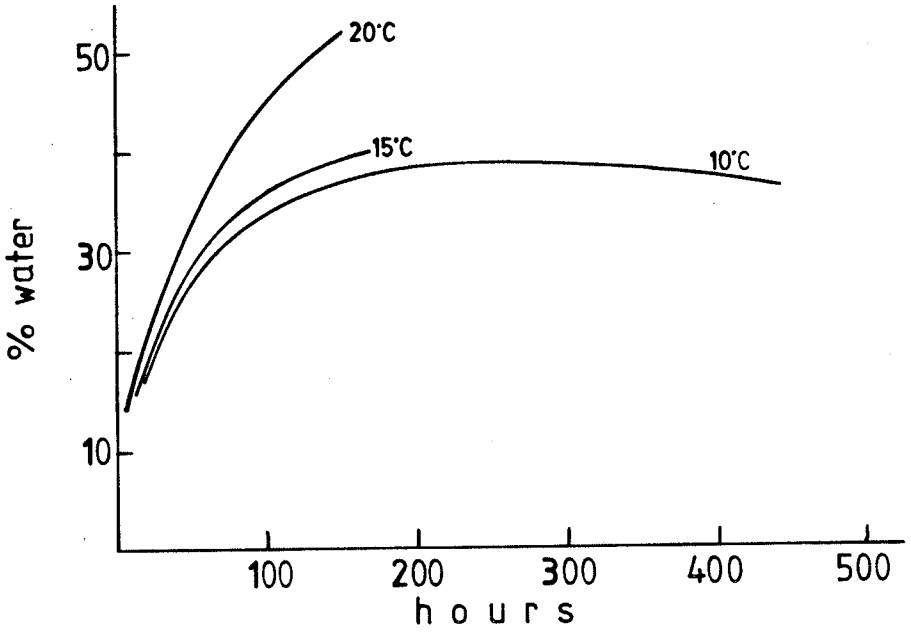


fig. 34. The effect of temperature on vapour uptake in medium-light Neepawa.

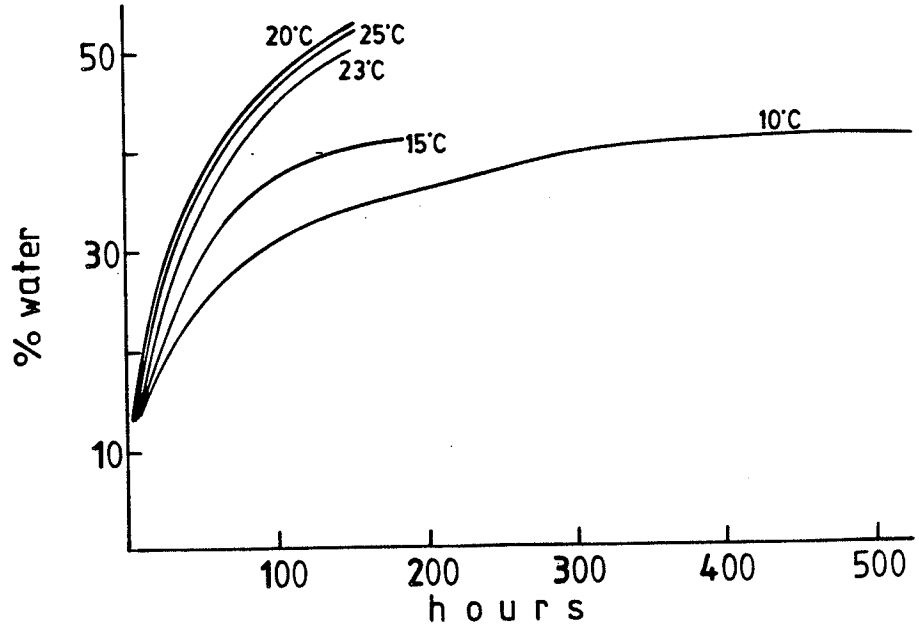


fig. 35. The effect of temperature on vapour uptake in medium-dense Neepawa.

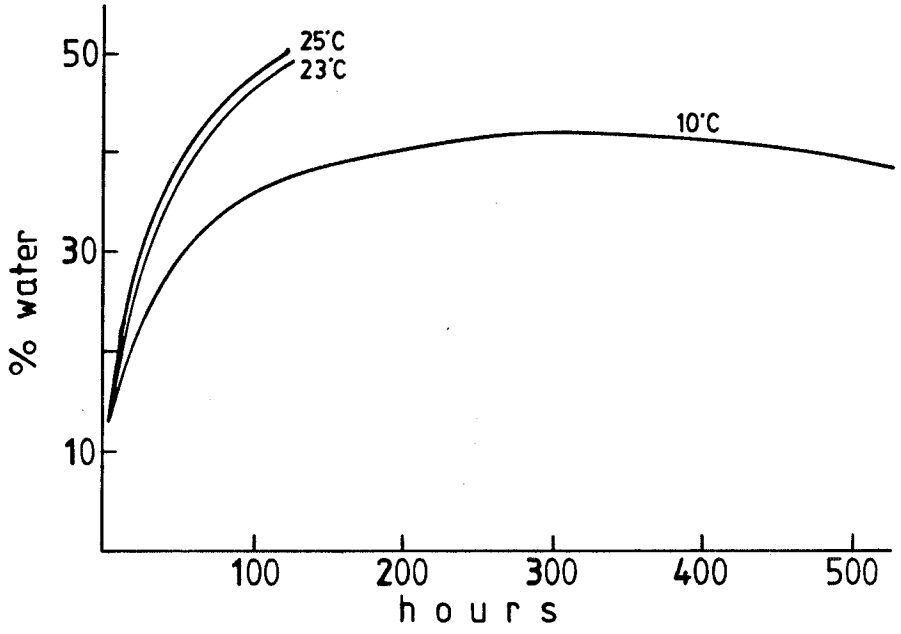


fig. 36. The effect of temperature on vapour uptake in large Neepawa.

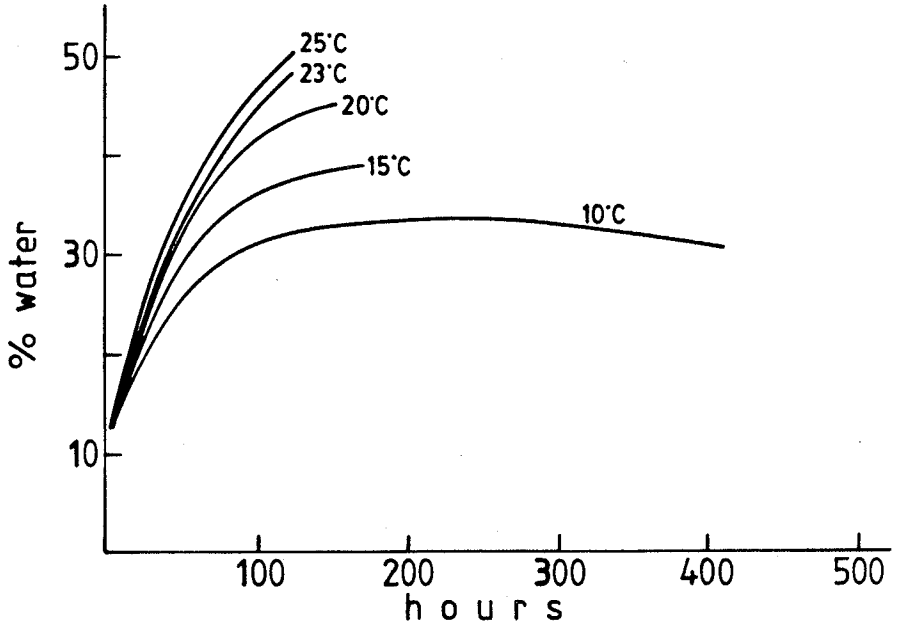


fig. 37. The effect of temperature on vapour uptake in medium Norstar wheat.

TABLE 3

R-square and Predicted Formulae for each seed type - temperature treatment

percent water = intercept + A(hours) + B(square root of hours)

	R squared	Intercept	A Hours	B Rt. hours
10 ML	0.882	9.04	-0.11	3.55
MD	0.883	9.97	-0.05	2.58
L	0.756	8.99	-0.11	3.79
NS	0.753	10.76	-0.10	2.98
15 ML	0.982	8.04	-0.16	4.46
MD	0.992	8.34	-0.16	4.45
NS	0.993	9.23	-0.14	4.05
20 ML	0.992	8.52	-0.15	5.28
MD	0.979	8.12	-0.15	5.44
NS	0.995	9.29	-0.14	4.71
23 MD	0.984	8.14	-0.20	5.67
L	0.991	8.55	-0.11	5.06
NS	0.983	8.49	-0.17	5.39
25 MD	0.987	8.82	-0.15	5.31
L	0.987	9.32	-0.13	5.36
NS	0.988	9.73	-0.14	5.12

As a rule, the various jars in a replicate complimented each other very well, that is, they were on or close to the predicted curve. In a few cases, one jar in the curve deviated from the rest. Such a deviation did not contain bends or bumps at different hour locations of those on the main curve. Rather, the whole curve was located at either higher or lower percent water values than those of the main curve. This would suggest error in the initial weighings during the set-up of the jar which affected all subsequent calculated water percent values. Jars with large deviations were omitted, while those with smaller deviations were included, since the deviations may well have been a seed sample rather than weighing effect. This resulted in somewhat lower R-square values.

It was obvious that temperature played the major role in determining uptake characteristics. Whereas at warmer temperatures, water content continued to rise, at 10 C water content levelled off or even dropped. At 300 hours when the 10 C curves more or less peaked, the percent water contents were 37.5, 39.7, 41.6 and 32.4 for the medium light, medium dense, and large Neepawa, and the Norstar respectively. At temperatures above 15 C, however, the uptake continued into germination. The values for Norstar tended to be lower than those for the Neepawa sizes, although significant differences were not always present. However, this would fit in well with the Norstar germination characteris-

tics (Experiment 6) in which germination occurred at lower water contents.

All data points for each treatment were plotted against the square root of hours (not shown). This resulted in a plot with more linear regions. Park (1968) used this method of plotting to determine if there were several different linear portions on a curve depicting solvent diffusion into polymer samples. It became quite apparent that the data did reveal two linear regions: the initial region where the increase in percent water was rapid, and a second region where uptake was slower (Fig. 38).

Table 4 shows the slopes of both regions for all the treatments as well as the location in square root of hours where the break between the two linear regions occurred. Given that the slope values are expressed as the increase in percent water/ $\sqrt{\text{hours}}$, it is important to realize that they differ from percent water/hour slopes, given that the two regions occur at different times.

Fig. 39 shows the slopes in both regions at all temperatures. It becomes obvious that temperature was the key determinant for slope in both regions. Seed type effects appeared to be non-significant, as slope values at a given temperature were relatively close together, and criss-crossed across the temperature range. Interestingly, the slope of the slopes across the temperature range was similar in both regions; 0.136 and 0.164 increase in percent water per $\sqrt{\text{hour}}$ per C for region I and II respectively.

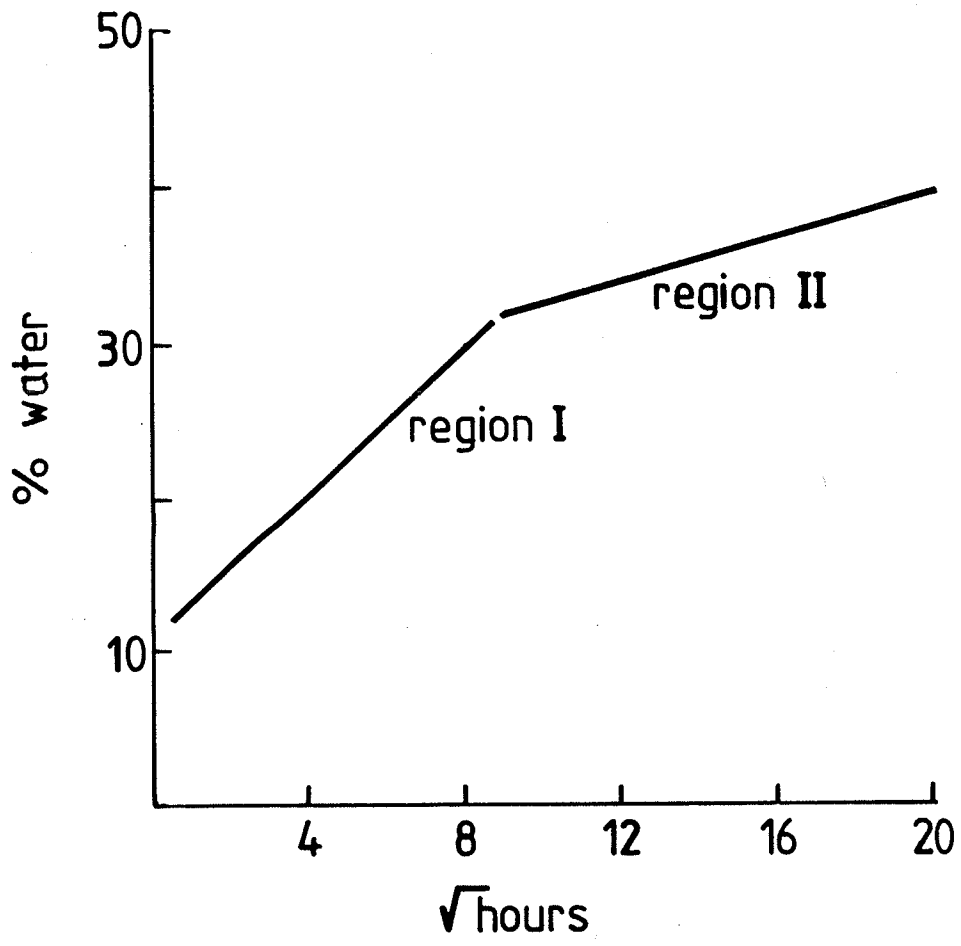


fig. 38. Curve containing typical linear regions when data is plotted against $\sqrt{\text{hours}}$.

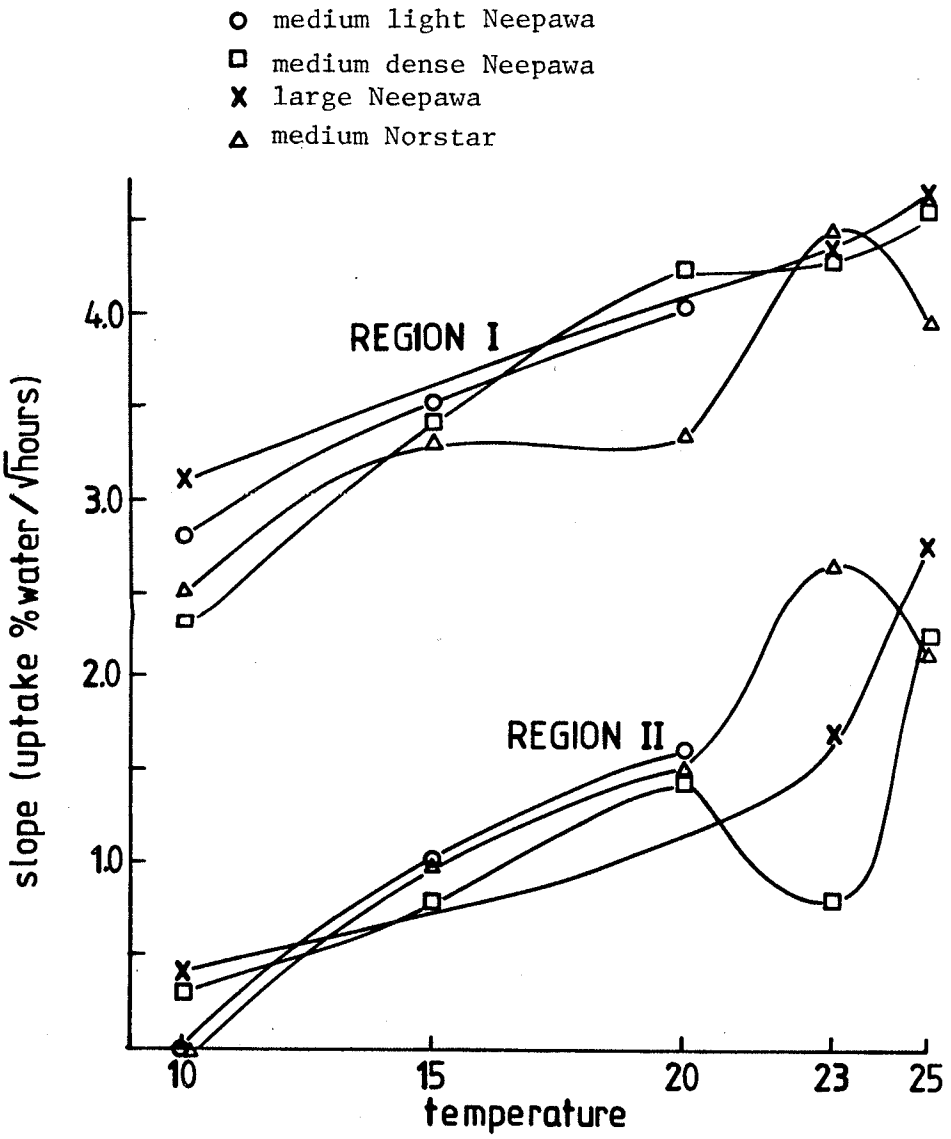


fig. 39. Water uptake slopes of region I and region II.

The R-square values for the calculated slopes were fairly respectable for all except the 10 C treatments. In the 10 C treatments, the region I R-squares were reasonably high, but in region II the values were terrible (see Table 4).

The location of the break between the two regions ranged from 7.5 to 11 $\sqrt{\text{hours}}$ (approximately 60 - 120 hours). The 10 C treatments had significantly higher time values than the other temperatures. This is due to slower uptake rates under cold conditions (Mohsenin 1970). The water content at the break was lowest at 10 and 15 C - about 35%. At warmer temperatures water contents were around 42%. The Norstar seeds generally had lower mean water contents at the break. Seemingly the Norstar has a lower capacity to take up water, since it also germinated at lower water contents (Experiment 6).

TABLE 4

Characteristics of Linear Regions of Vapour Phase Uptake

	location of break $\sqrt{\text{hours}}$	% water at break	Region I slope	R^2	sig	Region II slope	R^2	sig
10 C ML	10	35	2.80	0.890	0.01	-0.03	0.000	0.01
MD	11	35	2.29	0.864	0.01	0.29	0.257	0.05
L	9.5	37	3.19	0.811	0.01	0.35	0.043	ns
NS	9	31.5	2.52	0.889	0.01	-0.15	0.029	ns
15 C ML	7.5	33	3.53	0.993	0.01	1.02	0.783	0.01
MD	8.5	36	3.41	0.990	0.01	0.83	0.966	0.01
NS	7.5	32	3.28	0.995	0.01	1.06	0.966	0.01
20 C ML	9	46	4.02	0.996	0.01	1.59	0.904	0.01
MD	8	42	4.25	0.985	0.01	1.48	0.850	0.01
NS	9	40.5	3.39	0.987	0.01	1.48	0.944	0.01
23 C MD	8.0	42	4.28	0.987	0.01	0.82	0.951	0.01
L	8.0	45	4.32	0.993	0.01	1.70	0.940	0.05
NS	7.5	40	4.37	0.973	0.01	2.66	0.944	0.01
25 C MD	8.0	42	4.52	0.986	0.01	2.19	0.864	0.01
L	7.5	43	4.64	0.993	0.01	2.70	0.780	0.01
NS	8.5	43	3.90	0.984	0.01	2.80	0.602	0.05

10.4.4 C: Vapour Phase Germination Results

Vapour phase germination only occurred after extended periods of time as water uptake was slow. Since vapour uptake is slow and cold temperatures further depress it (Mohsenin, 1970), the germination potential under these conditions was so greatly reduced, that germination never occurred at temperatures of 15 C and lower. Although the 10 and 15 C experiments lasted for 25 and 20 days respectively, not one seed germinated. Experiments were stopped at that time, since the seeds had long ago stopped gaining appreciable amounts of water, and in some cases were even losing weight. The reduction of weight could have been due to seed and/or microbial respiration. In a few cases fungal mycelia were observed in spite of the fungicide treatment. In these cases, jars were immediately removed from the experiment. The psychrophilic fungi tend to invade the germ and aleurone preferentially, possibly because of high lipid contents in these tissues. This could kill the embryo.

Although the correlation between hours and percent water in the previous section of this experment was quite good, good correlations relating to germination were not always present as is evident by some high L.S.D. values. A major part of the problem was due to the fact that accurate germination counts could not be taken, since all but the final count depended on looking through the sides of a glass jar which greatly distorted the view. Even though the seeds

were weighed very regularly, in several cases germination was already well underway before it was noticed. Consequently, time and water content values at the end of the lag and 50% germination were not very accurate. In spite of the fact that significance could not always be attained due to the high L.S.D. values, interesting trends are nonetheless presented.

All the hour and percent water values in Table 5 represent the mean value of all replicates. The individual values were calculated using linear regression on the closest points surrounding the desired target. The 23 C results were omitted since in many of the jars germination was almost complete before it was discovered, making valid calculations impossible.

Table 5 shows the germination results at 20 and 25 C for both end of lag and 50% germination. As in Experiment 6, the Norstar germinated sooner and at lower water content than the Neepawa seeds. Lag time accounted for 75 to 90% of hours to 50% germination. The end of the lag period occurred at about 48.5 and 41.7% water respectively for the Neepawa and Norstar seeds. In Experiment 6, where the seeds were germinated on moist sand, the end of the lag period in the 23 C treatment occurred at about 51.0 and 37.5% water respectively for the Neepawa and Norstar seeds. The slower water uptake associated with the vapour phase experiments

TABLE 5

Vapour Phase

Hours and Percent Water (d.w. basis)
at the end of the Lag Period and
50% Germination (mean values)

	end of lag				50% Germination			
	Hours	LSD	% Water	LSD	Hours	LSD	% Water	LSD
20 C.								
ML	123	6.2	47.7	13.1	162.5	14.8	51.6	7.6
MD	125.5	1.7	51.1	9.8	168.0	10.2	52.0	0.7
NS	115.5	1.7	42.5	3.4	136.0	13.6	44.4	2.9
25 C.								
MD	85.3	1.7	46.6	2.0	99.8	3.4	49.4	0.5
L	89.7	3.4	48.1	1.2	99.9	5.1	49.2	0.8
NS	53.5	6.8	40.9	1.7	70.5	5.0	44.0	2.7

* L.S.D. values at p=0.05

appeared to reduce the initial water requirement in the Neepawa seeds but slightly increased it in the Norstar. Vapour phase uptake allowed more water to equilibrate with the seed given its slow nature. This would likely result in lower embryo and higher endosperm water contents, since as seeds take up water, the embryo wets faster than the endosperm (Stenvert and Kingswood, 1976).

The overall mean increase in the percent water from the end of the lag period to 50 percent germination was 2.3 percent. The mean increase in Experiment 6 was about 5%. There was no difference in the pattern of the Norstar and

Neepawa treatments. Since due to higher equilibrium, the endosperm would have a higher water content and only a small amount of extra water for the embryo would be required to induce germination. All regions within the seed reached the minimum critical water content. Moreover, despite all efforts being made in the sand experiment to provide equal uptake opportunity, it is likely that some seeds had better contact with the sand water than others, resulting in less uniformity of germination, and hence a greater calculated increase in water after the lag time.

Chapter XI

EXPERIMENT VIII - DYE EXPERIMENT

11.1 INTRODUCTION

Campbell (1958), after noticing rapid hydration of the dorsal endosperm region in Manitoba but not in British wheats, suggested that the cause might be mechanical damage to the pericarp which would enable water to move rapidly beneath it by capillary action. He immersed the brush end of damaged wheat kernels into a dye solution whereupon the dye entered under the pericarp and rapidly moved along the dorsal side to the embryo. Thus mechanical damage could be a source of variability in germination studies.

Possibly, damage to the brush end of the seed could occur not only during machine harvest and handling, but also during maturation and drying under suitable environmental conditions.

11.2 MATERIALS AND METHODS

A dye uptake experiment in which seeds placed on filter paper in petri plates containing a dye solution was conducted. Petri plates a few mm. larger than the diameter of 9 cm. Whatman no. 1 filter discs were used. The extra margin was needed as the paper expanded upon wetting. One

to four discs were placed in the petri plates which were located on a horizontal surface. A dye solution containing a 1:10 dilution of black ink (Osmiroid) was created. Four ml. of this solution was carefully pipetted into each petri plate. Any air bubbles underneath the filter paper were carefully removed. A fairly constant depth of solution was achieved by this technique. Seeds were placed crease down on the filter paper, at least 1 cm. apart from each other and 1 cm. from the paper edge. Not more than 25 seeds were ever placed in each dish, since too many seeds would lower the depth of the solution caused by water held in the meniscus around seeds. The ink appeared to be non-toxic and did not appear to strain tissues.

11.2.1 Part A

Machine-harvested and hand-picked Neepawa and hand-picked Glenlea were placed on a filter disc with 4 ml. solution. Dye entry was observed.

11.2.2 Part B

Machine-harvested Neepawa, Leeds, and Columbus cultivars were placed on one to four filter discs with a constant 4 ml. solution. Dye entry was observed.

11.2.3 Part C

Using the scanning electron microscope, the collar-brush region of both Leeds and Neepawa wheat kernels were examined. In many wheats, the brush region is set off from the dorsal region by the so-called 'collar' which essentially is a fold in the pericarp. According to Bradbury et al. (1956), most wheats have an air space in this region. Since hexaploid wheats have a dense mass of long hairs compared to durum wheats which have fewer shorter hairs, the durum wheat Leeds was examined. With Neepawa, the brush had to be burned away by quickly passing seeds several times through a flame to expose the region.

11.3 RESULTS AND DISCUSSION

11.3.1 Part A

Machine harvested Neepawa wheat showed dye entry within 5 minutes. Hand-picked Glenlea kernels under the same conditions showed no dye uptake even at 30 minutes. However, hand-picked Neepawa did show dye entry within several minutes (Fig. 40). While mechanical damage caused by harvesting and handling may be involved, drying of the pericarp under certain conditions or in some cultivars could result in a crack or a tear of the pericarp at the brush end.

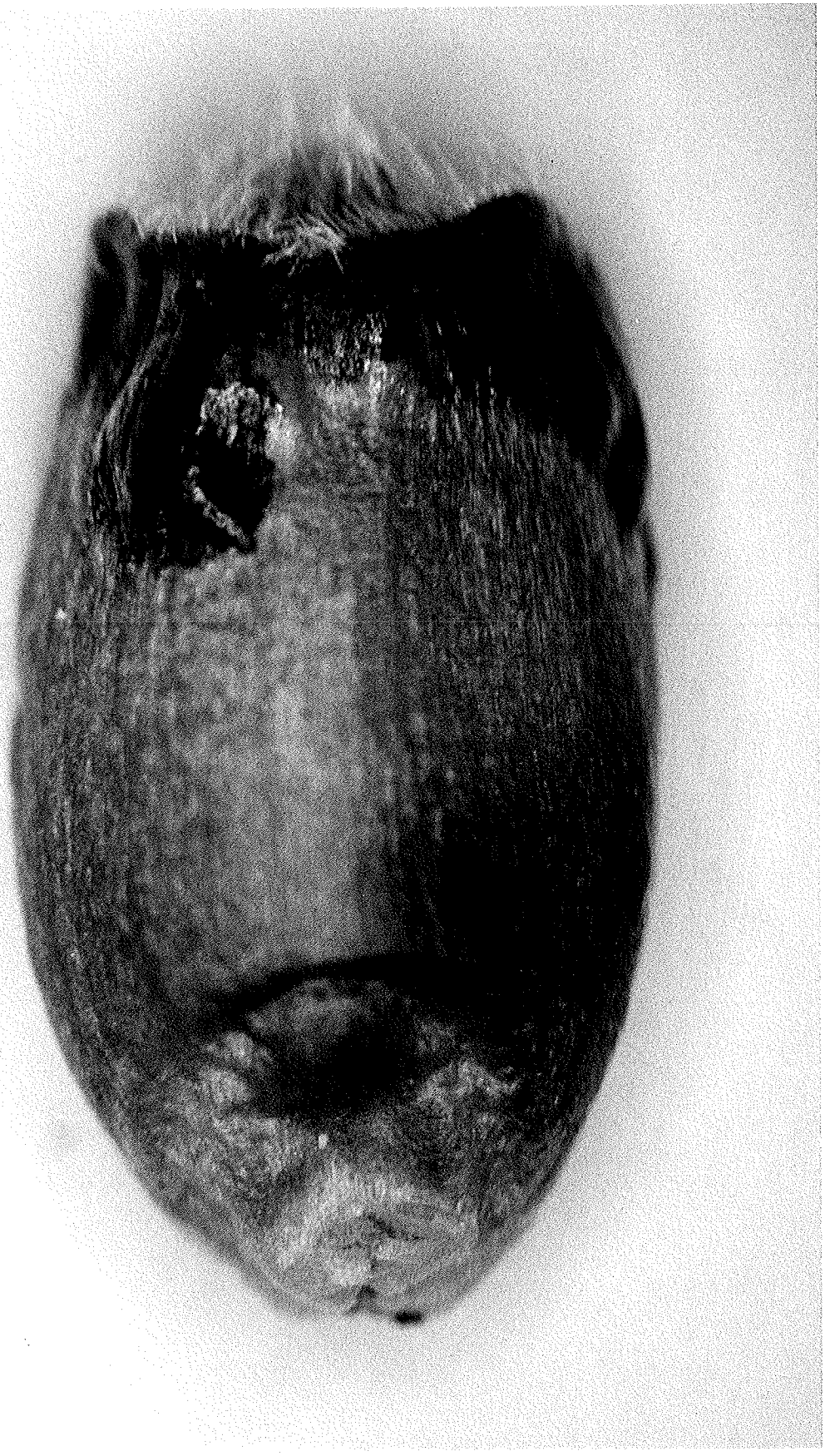


Fig. 40. Neepawa kernel showing dye entry at brush-end.

11.3.2 Part B

Table 6 shows typical results of seeds showing dye entry with various varieties and filter paper numbers. The number of seeds showing dye entry increased with incubation time but generally did not increase beyond 70%, even after four hours. With three filter papers, the surface of the paper was barely wet, and dye entry was absent or very low. With four papers it was never observed. Under "wetter" conditions, a meniscus formed around each seed and the dye solution could be observed to rise by capillary action through the brush: Initial dye movement beneath the pericarp involved an abrupt filling of the air space beneath the collar. Movement along the dorsal surface involved a swelling of the pericarp. Apparently, the attachment of the pericarp to the seed is weaker in the dorsal region than elsewhere.

TABLE 6

Number of Seeds (of Ten) showing dye entry under the Pericarp in the Brush Region at 15 minutes

Filter papers	Neepawa	Leeds	Columbus	Neepawa*
1	3.7	2.3	2.0	3.0
2	3.7	2.0	0	0
3	0	0	0	0
4	0	0	0	0

*column 1, bulk sample; column 4; medium size.

These results demonstrate that dye can move beneath the pericarp in a significant number of seeds under usual seed germination test conditions. Differences between varieties could be due to variation in seed shape and size and in the waxiness or roughness of the seed coat. These variables could determine the extent of dye solution uptake in the brush region. In the field, varieties with more relaxed glumes might allow accumulation of liquid water around the brush. If the collar is cracked the water may move rapidly beneath the pericarp to the embryo. Whether or not this water results in sprouting could be determined by presence or absence of water soluble inhibitors in the glumes and in the pericarp.

11.3.3 Part C

The scanning election microscope showed a crack or a tear in many of the Leeds seeds, usually within the fold of the collar (Fig. 41). Similar cracks were observed in Neepawa seeds after the brush was burned away, but it is not known whether the heat altered the structure.

In milling of wheat, the grain is tempered; that is, moisture content is raised to 16-18% and the moisture is allowed to equilibrate throughout the grain. This "mellows" the endosperm so that less energy is needed to produce flour. But it also "toughens" the bran so that it remains in large pieces which can be easily separated from the

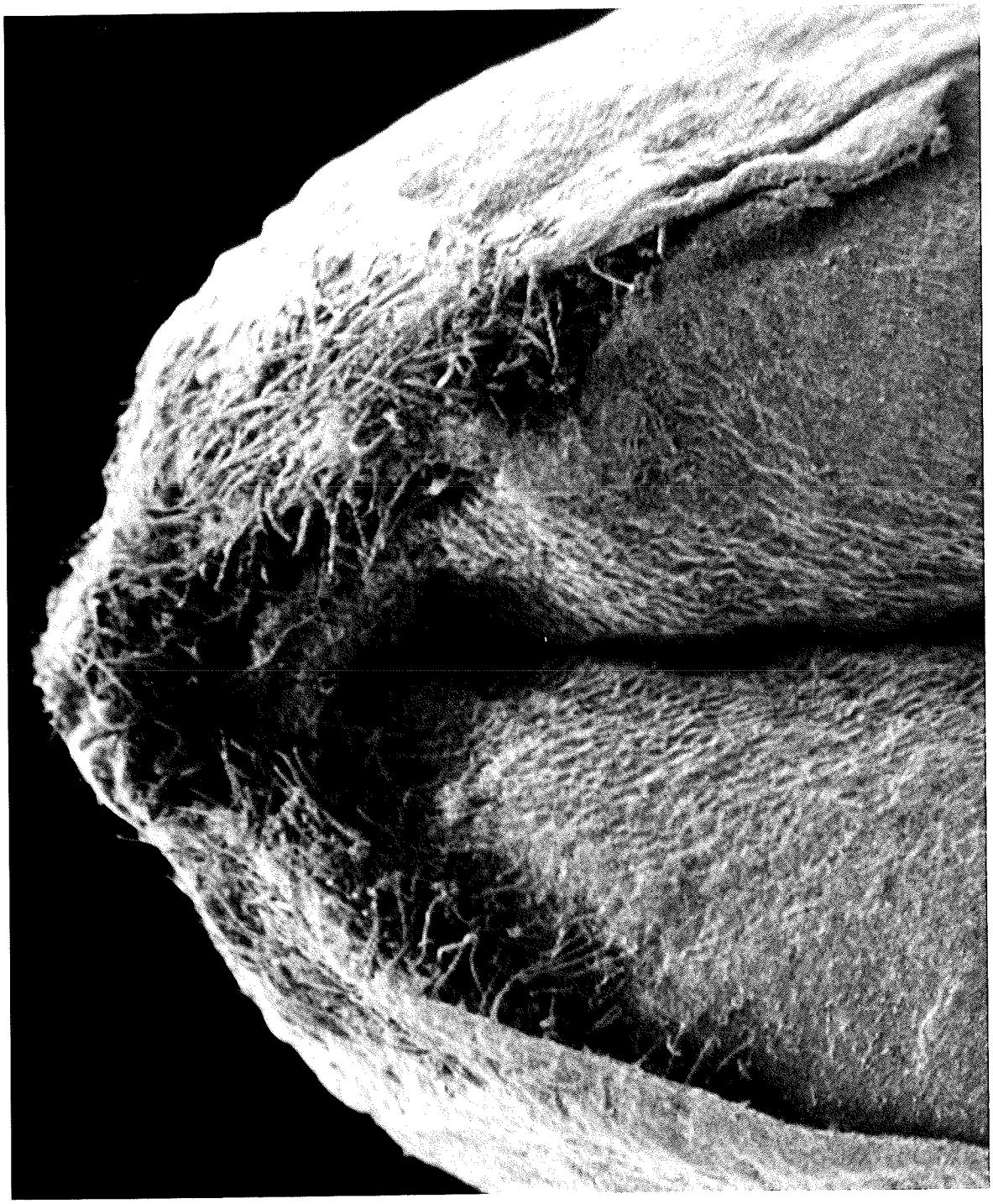


Fig. 41. Leeds kernal magnified at brush end showing collar region and crack.

flour. Rate or temperature of drying could determine whether or not the crack is developed.

Chapter XII

GENERAL DISCUSSION

Water plays an important biological as well as physical role in the seed. Physical seed characteristics as influenced by water will be greatly affected by the rate of entry and temperature. Rapidly wetted seeds show distinct wet and dry regions (Waggoner and Parlange, 1976). At lower seed water contents, the extent of equilibrium will determine the amounts of bound and free water (Becker and Sallans, 1956). As well, water content at any region in the seed will determine if that region is rigid or plastic in nature (Campbell and Jones, 1955). Non-uniform moisture distribution in the seed results in a strain between the regions due to uneven pressures. Lower temperatures will result in higher binding and slower movement (Mohsenin, 1970), which would increase the stress. The lack of equilibrium in such a situation is likely one of the factors responsible for the inability of warm temperature crops to germinate in cold conditions (Khan, 1977) due to a damaged seed structure.

Since water is the first prerequisite for germination, more knowledge on where the water is located and how it moves into and within the seed is essential to under-

standing the expression of dormancy. Experiments were conducted by controlling uptake at various temperatures and external hydraulic conductivities. As well, location of water entry was controlled by the various seed placements. This was done in an attempt to see how germination might be influenced or controlled by seed structure.

Seed structural characteristics such as the proportion of protein, pentosan, and starch (Stenvert and Kingswood, 1977), the degree of mealiness (Hinton, 1955), internal fracturing caused by freezing-thawing or wetting-drying cycles (Briggs, 1978), and brush region damage (Campbell, 1958) all would directly or indirectly affect water uptake, water movement, seed plasticity, and seed swelling pressures.

Variations in protein content would provide a feasible explanation for the different germination times and water contents between the Neepawa and Norstar wheats. As is generally the case, the hard red spring Neepawa had a higher protein levels than the Norstar winter wheat. Bushuk (1966) determined that water affinity for wheat protein was several times that shown by undamaged starch. Stenvert and Kingswood (1977) determined that high protein slowed down water movement to more internal regions. This consequently would delay germination, as protein would have to be "saturated" before internal regions received their water. Varietal differences in quantity or quality of seed protein as well as

variations between seed lots within a variety could be influential.

The pericarp has to dry in order for the seed to become germinable (Mitchell et al., 1980). Consequently air channels beneath the pericarp are formed. Conditions during drying would influence the formation of these channels as well as damage to the brush-collar region. Pollock, et al. (1955) determined that water sensitivity could be overcome by removal of the pericarp. Coumarin-treated non-dormant seeds and post-harvest dormant seeds behaved similarly in that they did not germinate readily under wet conditions. The dye experiment showed that substantial numbers of seeds took up water at the brush-collar region and that movement proceeded toward the embryo beneath the pericarp within a matter of minutes. This movement in the air channels could not only provide a rapid route for water transfer toward the embryo, but also for inhibitors present in the pericarp. Under conditions of excess water, not only would water entry and movement be rapid, but a greater proportion of the water reaching the embryo could come from this route, thereby increasing the significance of pericarp inhibitors, whether they be natural or applied like the coumarin. In non-dormant seeds, sufficient levels of pericarp inhibitors would be modified or lost, eliminating any associated inhibitory effects. Conditions during maturation could alter the effectiveness of pericarp inhibitors by influencing pericarp structure and brush damage.

It is a fundamental of polymer science that polymers have a memory. Conformation and properties of a particular polymer will depend on its past history (Suggett, 1975). External water and temperature conditions, both during maturation and imbibition, will influence the conformation of seed polymers which may subsequently affect germinability.

These subtle structural changes in response to external factors may provide a mechanism for the seed's ecological survival. Most work on seed dormancy and sprouting resistance is centered on the hypothesis that inhibitor-promoter interactions are the limiting factor but it is clear that physical properties of the seed may modify the response.

Chapter XIII

SUMMARY AND CONCLUSIONS

Both the moist sand system and vapour phase experiments were designed to impose resistance to water movement outside the seed itself. Under these conditions, moisture uptake and germination characteristics were different than if seeds contacted liquid water. As well, colder temperatures similiar to those found in spring soils, were included in the study.

External hydraulic conductivity played a crucial role in determining seed water availablity and germination. Sand which had excess water on the surface, and hence a very high hydraulic conductivity, resulted in rapid water uptake and germination in non-dormant seeds, compared to sand having only bound water. In sands having bound water, if seeds remained at their original position on the sand, hydraulic conductivity around the seed diminished with uptake. Increased temperatures resulted in decreased water contents at 50% germination. If, however, seeds were moved about during uptake, new higher hydraulic conductivities were created, which in turn resulted in higher water contents at 50% germination with increases in temperature. Higher seeding densities and larger seeds depleted sand water sooner, thereby

lowering sand hydraulic conductivity. This, in turn, delayed germination. Larger seeds also required more water, further increasing the delay.

Increased temperatures resulted in decreased germination time, primarily by decreasing the lag period. In semi-dormant seeds, a temperature increase resulted in less of a time decrease, apparently due to a slower water uptake rate.

Neepawa wheat was slower to germinate than the Norstar, basically due to increased lag time. This appeared to be due to higher water requirements in the Neepawa. The higher protein content of the Neepawa was likely responsible for this.

Vapour phase uptake, given its slow nature, gave seeds greater opportunity to reach water equilibrium. This is evident in that the water increase from the end of lag to 50% germination was only about 2-1/2% compared to the 5% observed in the sand study. Vapour uptake prior to germination underwent two phases. The first phase was quite rapid, especially at warmer temperatures. The second phase was more gradual. At colder temperatures, uptake was hardly noticeable in the second phase.

Germination inhibition of seeds containing either post-harvest dormancy or coumarin treatment only occurred under conditions in which seeds contacted liquid water. The only exception to this was in one sample of dormant seeds

placed on semi-moist sand brush-end down, in which inhibitors found in the pericarp likely moved to the embryo, causing the inhibition. A lack of air channels caused by insufficient drying apparently was not responsible since water uptake rates were reasonable. The dye experiment clearly demonstrated that uptake can occur regularly at the brush end of the seed and proceed underneath the pericarp. The scanning electron micrograph gave clear evidence of a crack at the collar region which would allow water entry. Water movement underneath the pericarp toward the embryo may provide a key control mechanism of dormancy, as it could provide a key route for pericarp inhibitors to the embryo. Unfortunately, non-dormant coumarin-treated brush-down seeds did not display strong inhibition. Since acetone was used in applying coumarin to seeds, it is possible acetone-soaking rearranged surface waxes and phenols to the capillary space beneath the pericarp, thereby affecting water movement.

In the past, most germination and dormancy studies have been interpreted in terms of membranes and inhibitor-promoter interactions. However, seed structure and the way water and temperature interact with it, may be equally important. Almost all previous work has been done in conditions where seeds contacted liquid water and room temperatures, conditions not naturally common. The present work shows that dormancy is most strongly expressed when the seed

is in contact with liquid water and at higher temperatures. Other workers have shown that dormancy in wheat, oats, and barley is only expressed at temperatures above some critical value. It is possible that other types of dormancy exist but they have been overlooked because research methodology would preferentially select this one type of dormancy. The use of damp sand at lower temperatures would provide a means for searching for other types of dormancy.

Chapter XIV

ADDENDUM

After the oral examination of this thesis was completed, further analysis of data from Experiment VI revealed an interesting trend involving seed density and temperature effects on the post-lag germination rate and water uptake rate. Figure 42 shows the germination and water uptake rates of the three Neepawa fractions. The greatest difference between curves occurred with the medium light and dense fractions. In light seeds, both germination and water uptake rates increased linearly between 8 and 15 C but levelled off with a further temperature increase. In the dense seeds, on the other hand, germination rates decreased from 8 to 12 C, and only at warmer temperatures did the germination rate rise. Water uptake rate in the dense seeds slowly increased from 8 to 15 C, but accelerated from 15 to 23 C. Both light and dense seeds showed similar post-lag germination and water uptake rates at 23 C. Both the large Neepawa, and the Norstar (curve not shown) appeared to have a "hybrid" curve displaying characteristics of both light and dense curves. This is logical, as both the large Neepawa and medium Norstar seeds were not further subdivided into light and dense fractions as the medium Neepawa was.

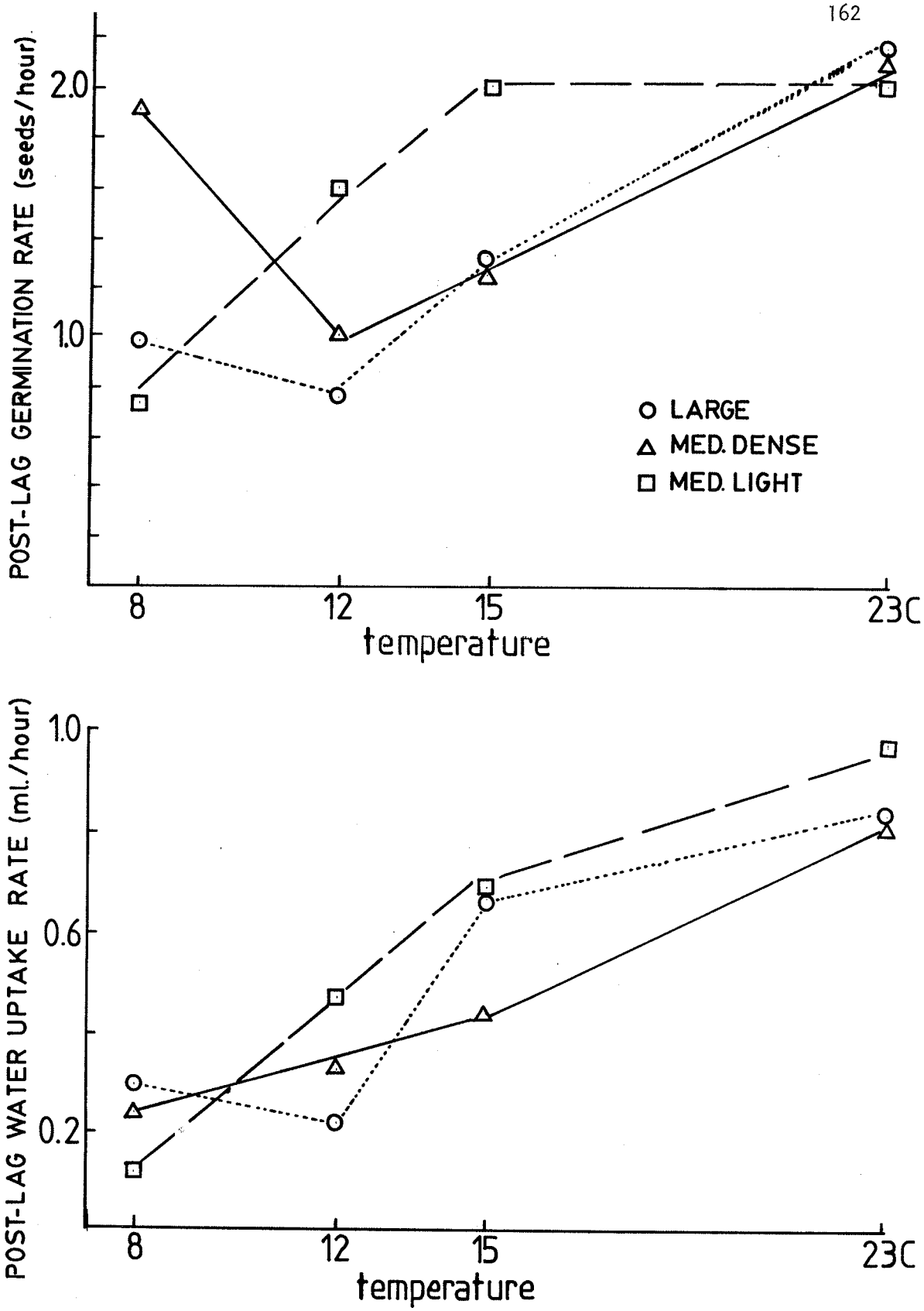


Fig. 42. Post-lag rate of germination and water uptake in three fractions of Neepawa wheat.

The different behaviour of light and dense fractions may be explained in terms of endosperm fissuring. Light seeds, which would have more fissures, would have unbound water moving in the capillary channels. This movement should be less temperature-dependent. In dense seeds fewer fissures would force more water to move in the bound phase. Such water movement would have a large Q10.

It is important to remember, however, that temperature effects played a much greater role prior to germination during the lag time, and that water uptake here determined percent water during germination.

LIST OF REFERENCES

Adamson, 1967. Physical Chemistry of Surfaces, 2nd ed. John Wiley and Sons, New York.

Andrews, C.J. and Burrows, V.D. 1972. Germination response of dormant seeds to low temperature and gibberellin. Can. J. Plant Sci. 52: 295-303.

Babbitt, J.D., 1949. Observations on the absorption of water vapor by wheat. Can. J. Res. 24f: 52-72.

Babenhuizen, N.P., 1946. On the swelling of starch grains. Trans. Faraday Soc. 42b: 255-259.

Bassiri, M., Khosh-Khui, M., and Rouhani, I. 1977. The influences of simulated moisture stress conditions and osmotic substrates on germination and growth of cultivated and wild safflowers. J. Agri. Sci., Camb. 88: 95-100.

Becker, H.A. and Sallans, H.R. 1956. A study of the desorption isotherms of wheat at 25 C and 50 C Cereal Chem. 33: 79-91.

Becker, H.A., 1960. On the absorption of liquid water by the wheat kernel. Cereal chem. 37: 309-323.

Belderok, B. 1976a. Physiological-biochemical aspects of dormancy in wheat. Cereal Res. Commun. 4: 133-138.

_____. 1976b. Changes in the seed coat of wheat kernels during dormancy and after ripening. Cereal Res. Commun. 4: 165-172.

Bewley, J.D. and Black, M. 1978. Physiology and Biochemistry of Seeds. Springer-Verlag, Berlin.

Blacklow, W.M., 1972. Mathematical description of the influence of temperature and seed quality on imbibition by seeds of corn (Zea mays L.). Crop Sci. 12: 643-646.

Blackshaw, R.E., Stobbe, E.H., Shaykewich, C. F. and Woodbury, W. 1981. Influence of soil temperature on green foxtail establishment in wheat. J. Weed Sci. Soc. Amer. 29: 179-184.

Bradbury, D. MacMasters, M.M., and Cull, I.M. 1956. Structure of the mature wheat kernel. Cereal Chem. 33: 330-373.

Brady, N.C. 1974. The Nature and Properties of Soils. 8th ed. MacMillan Publishing Co., Inc., New York, p. 164-199.

Briggs, D.E., 1972. Enzyme formation, cellular breakdown and the distribution of gibberellins in the endosperm of barley. Planta (Berl.). 108: 351-358.

Briggs, D.E. 1978. Barley. John Wiley and Sons, New York.

Brown, A.J., 1907. On the existence of a semi-permeable membrane enclosing the seeds of some graminae. Am. Bot. 21: 81-89.

_____., 1909. The selective permeability of the covering of the seeds of Hordeum vulgare. Roy.Soc. Proc. 81b: 82-93.

_____., and Worley, F.P., 1912. The influence of temperature on the absorption of water by seeds of Hordeum vulgare in relation to the temperature coefficient of chemical change. Roy. Soc. Proc. 85: 546-553.

_____., and Tinker, F. 1916. Selective permeability: the absorption of phenol and other solutions by the seeds of Hordeum vulgare. Roy. Soc. Proc. 89b: 373-379.

Brown, H. and Morris, A., 1890. Researches on the germination of some of the graminae. J. Chem. Soc. p. 458.

Bushuk, W., 1966. Distribution of water in dough and bread. Baker's Digest. 40: 38-40.

_____., and Winkler, C.A. 1957. Asorption of wheat flour starch and gluten. Cereal Chem. 34: 73-86.

Butcher, J. and Stenvert, N.L., 1973. Conditioning studies on Australian wheat. 3. The role of the rate of water penetration into the wheat grain. J. Sci. Fd. Agric. 24: 1077-1084.

Cal, J.P. and Obendorf, R.L., 1972. Differential growth of corn (Zea Mays L.) hybrids seeded at cold root zone temperatures. Crop Sci. 12: 572-575.

Campbell, J.D. and Jones, C.R., 1955. On the physical basis of the response of endosperm density to change in moisture content. Cereal Chem. 32: 325-343.

_____, and _____, 1957. The rates of penetration of moisture to different points in the central cross-section of the endosperm in damped Manitoba wheat grains. Cereal Chem. 34: 110-116.

_____. 1958. The effect of mechanical damage to wheat grains during scouring on their subsequent absorption of water during washing. Cereal Chem. 35: 47-56.

Clegg, M.D. and Easton, J.D., 1978. A thermogradient generating sand table. Agron. J. 70: 881-883.

Collins, E.J., 1918. The structure of the integumentary system of the barley grain in relation to localized water absorption and semi-permeability. Ann. Bot. 32: 381-414.

Collis-George, N. and Hector, J.B., 1966. Germination of seeds as influenced by matric potential and by area of contact between seed and soil-water. Aust. J. Soil Res. 4: 145-164.

_____., and Lloyd, J.E., 1979. The basis for a procedure to specify soil physical properties of a seed bed for wheat. Aust. J. Agric. Res. 30: 831-846.

_____., and Melville, M.D., 1978. Water absorption by swelling seeds. 2. surface condensation boundary condition. Aust. J. Soil Res. 168: 291-310.

_____., and Williams, J., 1968. Comparison of the effects soil matric potential and isotropic effective stress on the germination of Lactuca sativa. Aust. J. Soil Res. 6: 179-192.

DeJong, R. and Best, K.F., 1972. The effect of soil water potential, temperature, and seeding depth on seedling emergence of wheat. Can. J. Soil Sci. 59: 259-264.

Dubetz, S., Russell, G.C., and Anderson, D.T., 1962. Effect of soil temperature on seedling emergence. Can. J. Plant Sci., 42: 481-487.

Essery, R.E., Kirsop, B.H., and Pollock, J.R.A., 1955 Studies in barley and malt. 2. Tests for germination and water sensitivity. Inst. Brewing J. 61: 25-28.

Evans, M., Black, M., and Chapman, J., 1975. Induction of hormone sensitivity by dehydration is one positive role for drying in cereal seed. Nature. 258: 144-145.

Gosling, P.G., Butler, R.A., Black, M. and Chapman, J.M., 1981. The onset of germination ability in developing wheat. J. Expt. Bot. 32: 621-627.

Hadas, A., 1977. Water uptake and germination of leguminous seeds in soils of changing matric and osmotic water potential. J. Expt. Bot. 28: 977-985.

Hallem, P.M., 1981. Effects of soil temperature on root development in wheat. M.Sc. Thesis. U. of Manitoba.

Harper, J.L. and Benton, R.A., 1966. The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. J. Ecology, 54: 151-165.

Hegarty, T.W., 1972. Temperature relations of germination in the field. in W. Heydecker, ed. Seed Ecology. Pennsylvania State University Press.

_____., and Ross, H.A., 1978. Differential sensitivity to moisture stress of seed germination and seedling radicle growth in calabrese (Brassica oleracea var.italica) and cress (Lepidium sativum). Ann. Bot. 42: 1003-1005.

Hinton, J.J.C., 1955. Resistance of the testa to entry of water into the wheat kernel. Cereal Chem. 32: 296-305.

Hochachka, P.W. and Somers, G.M., 1973. Strategies of Biochemical Adaptation. W.B. Saunders Co., Philadelphia.

Hunter, J.R. and Dexter, S.T., 1950. Some seed-soil moisture studies with sugar beets. Proc. Amer. Soc. Sugar Beet Tech. 270-274.

Jansson, G., 1959. Chemically-induced water-sensitivity in barley seeds. Arkiv f. Kemi. 14: 279-289.

Jones, C.R. and Campbell, J.D., 1953. Micro-determination of endosperm density as a means of mapping moisture distribution in wheat. Cereal Chem. 30: 177-189.

Khan, A.A., 1977. Preconditioning, germination and performance of seeds. in A.A. Khan, Ed., The Physiology and Biochemistry of Seed Dormancy and Germination. North Holland Pub., Amsterdam, 283-318.

King, R.W., and Gale, N.S., 1980. Preharvest assessment of potential alpha-amylase production. Cereal res. Commun. 8: 157-165.

Krauss, L., 1933. Entwicklungsgeschichte der Fruechte von Hordeum, Triticum, Bromus, und Poa mit besonderer Beruecksichtigung ihrer Samenschalen. Jahrbuecher fuer Wissenschaftliche Botanik. 77: 733-808.

Lee, J.W. and Stenvert, N.L., 1973. Conditioning studies in Australian wheat IV. Compositional variations in the bran layers of wheat and their relation to milling. J. Sci. Fd. Agric. 24: 1565-1569.

MacKey, J., 1976. Seed dormancy in agriculture and nature. Cereal Res. Commun. 4: 82-91.

Manohar, M.S., 1966. Effect of "osmotic" systems on germination of peas (Pisum sativum L.). Planta (Berl.) 71: 81-86.

Menge, U., 1979. Rasterelektronenmikroskopische Untersuchungen zur Ermittlung mikromorphologischer und histologischer Kriterien fuer die unterschiedliche Auswuchsneigung von Weizenkaryopsen. Teil I: Entwicklung von Endosperm, testa, Perikarp von der Bluete bis zur Reife. Landbauforschung Voelkenrode. 29: 87-94.

Milner, M., and Shellenberger, J.A., 1953. Physical properties of weathered wheat in relation to internal fissuring detected radiographically. Cereal Chem. 30: 202-212.

Mitchell, B., Black, M., and Chapman, J. M., 1980. Drying and the onset of germinability in developing wheat grains., Cereal Res. Commun., 8: 151-156.

Mohsenin, N.N., 1970. Physical Properties of Plant and Animal Materials. Gordon and Breach Publishing, New York.

Moss, R., 1973. Conditioning studies in Australian wheat. II. Morphology of wheat and its relationship to conditioning. J. Sci. Fd. Agric. 24: 1067-1076.

Muchena, S.C. and Grogan, C.O., 1977. Effects of seed size on germination of corn (Zea mays) under simulated water stress conditions. Can. J. Plant Sci. 57: 921-923.

Nicholls, P.B., 1979. Induction of sensitivity of gibberellic acid in developing wheat caryopses: effect of rate of desiccation. Aust. J. Plant Physiol. 6: 229-240.

_____., 1980. Development of responsiveness to gibberellic acid in the aleurone layer of immature wheat and barley caryopses: effect of temperature. Aust. J. Plant Physiol. 7: 645-653.

Noll, J.S., and Czarnecki, E., 1980. Methods of extending the testing period for harvest-time dormancy in wheat. Cer. Res. Commun. 8: 233-238.

Owen, P.C., 1952. The relation of water absorption by wheat seeds to water potential. J. Expt. Bot. 3: 276-290.

Pawloski, M.C. and Shaykewich, C.F., 1972. Germination of wheat as affected by soil water stress. Can J. Plant Sci. 52: 619-623.

Peterson, R.F., 1965. Wheat, Botany, Cultivation, and Utilization. Interscience Publishers Inc., New York.

Peterson, J. R., and Cooper, P.G., 1979. Some considerations of water in the germination test. Seed Sci. Technol. 7: 329-340.

Pollock, J.R.A., Kirsop, B.H., and Essery, R.E., 1955. European Brewing Convention Congress, p. 203-211.

_____., 1962. The nature of the malting process. in A.A. Cook, Ed., Barley and Malt. Academic Press.

Roberts, E.H. and Smith, R.D., 1977. Dormancy in the pentose phosphate pathway. in A. A. Khan, ed., The Physiology and Biochemistry of Seed Dormancy in Germination. North Holland Publishing Co., Amsterdam.

Sedgley, R.H., 1963. The importance of liquid-seed contact during the germination of Medicago tribuloides desr. Aust. J. Agric. Res. 14: 646-653.

Shaykewich, C.F., and Williams, J., 1971a. Resistance to water absorption in germinating rapeseed (Brassica napus L.). J. Expt. Bot. 22: 19-24.

_____., and _____. 1971b. Influence of hydraulic properties of soil on pre-germination water absorption by rapeseed. (Brassica napus). Agron. J. 63: 454-457.

Shaykewich, C.F., 1973. Proposed method for measuring swelling pressure of seeds prior to germination. J. Expt. Bot. 24: 1056-1061.

Shelef, L. and Mohsenin, N.N., 1966. Moisture relations in germ, endosperm, and whole corn kernel. Cereal Chem. 43: 347-353.

_____., and _____., 1968. Effect of moisture content on mechanical properties of shelled corn. Cereal Chem. 46: 242-253.

Shull, C.A., 1920. Temperature and rate of moisture intake in seeds. Botanical Gaz. 69: 361-390.

Stenvert, N.L. and Kingswood, K., 1976. An autoradiographic demonstration of the penetration of water into wheat during tempering. Cereal Chem. 53: 141-149.

_____ and _____., 1977. Factors influencing the rate of moisture penetration into wheat during tempering. Cereal Chem. 54: 627-637.

Stout, B.A., Snyder, F.W., and Carleton, W.M., 1956. The effect of soil moisture and compaction on sugar beet emergence. Journal of the A.S.S.B.T. 9: 277-282.

Stoy, V. and Sundin, K., 1976. Effects of growth regulating substances in cereal seed germination. Cereal Res. Commun. 4: 157-163.

Suggett, A., 1975. Polysaccharides. in F. Franks, Ed., Water, Vol. 4. Plenum Publishing Co., New York.

Tanaka, T., 1981. Gels. Scientific Amer. 244: 124-138.

Takahashi, N., 1980. Effects of the environmental factors during seed formation on the pre-harvest sprouting. Cereal Res. Commun. 8: 175-184.

Taylor, S. and Ashcroft, G., 1972. Physical Edaphology. W. H. Freeman & Co., New York. p. 188.

Thill, D.C., Schirman, R.D., and Appleby, A.P., 1979. Osmotic stability of mannitol and polyethylene glycol 20,000 solutions used as seed germination media. Agron. J. 71: 105-108.

Thompson, P.A., 1970. Germination of species of Caryophyllaeae in relation to their geographic distribution in Europe. Ann. Bot. 34: 427-449.

Vegis, A., 1964. Dormancy in higher plants. Annu. Rev. Plant Physiol. 15: 185-224.

Waggoner, P.E. and Parlange, J., 1976. Water uptake and water diffusivity of seeds. Plant Physiol. 57: 153-156.

Wareing, P.F., van Staden, J., and Webb, D.P., 1972. Endogenous hormones in the control of seed dormancy. in W. Heydecker, ed., Seed Ecology. Pennyslvania State University Press.

Wellington, P.S., and Durham, V.M., 1961. Studies on the germination of cereals. 3. The effect of the covering layers on the uptake of water by the embryo of the wheat grain. Ann. Bot. 25: 185-196.

Yoshida, T., Yamada, K., Fujino, S., and Koumegawa, L., 1979. Effect of pressure on physiological aspects of germinating barleys and quality malts. J. Amer. Soc. Brewing Chem. 37: 77-84.

Appendix A

TABLES

TABLE 7

The effect of seed size and position (crease down or random drop on hours to 50% germination

	d.f.	s.s.	m.s.	F-value	PR>F
Model	11	1099.44	99.95	13.52	0.0001
Error	60	443.42	7.39		
Corrected Total	71	1542.86			
	R-square=0.713		C.V.=5.22		

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Position	1	47.857	47.857	6.48	0.0135
Size	5	1028.856	205.771	27.84	0.0001
Position*Size	5	22.732	4.546	0.62	0.6909

TABLE 8

The effect of varying amounts of sand water and seed size on hours to 50% germination.

	d.f.	s.s.	m.s.	F-value	PR>F
Model	25	14374.28	574.97	67.54	0.0001
Error	111	945.01	8.51		
Corrected Total	136	15319.29			
	R-square 0.938			C.V.=4.86	

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Water	12	7322.27	610.19	71.67	0.0001
Size	1	5861.73	5861.73	688.51	0.0001
Water*size	12	1190.29	99.19	11.65	0.0001

TABLE 9

The effect of various seeding densities using two seed sizes on hours to 50% germination

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	4961.477	708.783	88.10	0.0001
Error	32	251.443	8.045		
Corrected Total	39	5218.920			

R-square=0.951 C.V.=4.625

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	1	3773.89	3773.89	469.09	0.0001
Density	3	467.10	155.70	19.35	0.0001
Size*Density	3	720.49	240.16	29.85	0.0001

TABLE 10

The effects of seed position and chemical treatment on hours of 50% germination and water content at 50% germination in Neepawa wheat.

HOURS

	d.f.	s.s.	m.s.	F-value	PR>F
Model	8	6895.98	862.00	39.12	0.0001
Error	39	859.34	22.03		
Corrected Total	47	7755.32			

R-square=0.889 C.V.=8.72

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Treatment	2	822.87	441.44	18.67	0.0001
Position	2	6055.90	3027.95	137.42	0.0001
Treatment* Position	4	17.21	4.30	0.20	0.9394

WATER

	d.f.	s.s.	m.s.	F-value	PR>F
Model	8	540.04	67.50	21.06	0.0001
Error	39	125.03	3.21		
Corrected Total	47	665.07			

R-square=0.812 C.V.=3.03

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Treatment	2	308.90	154.45	48.18	0.0001
Position	2	186.82	93.41	29.14	0.0001
Treatment* Position	4	44.33	11.08	3.46	0.0164

TABLE 11

The effects of seed position and chemical treatment on hours to 50% germination and water content at 50% germination in Norstar wheat

HOURS

	d.f.	s.s.	m.s.	F-value	PR>F
Model	8	2213.0	276.63	310.4	0.0001
Error	9	8.0	0.89		
Corrected Total	17	2221.1			

R-square=0.996 C.V.=2.46

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Treatment	2	28.6	14.3	16.0	0.0011
Position	2	2170.5	1085.3	1217.9	0.0001
Treatment* Position	4	14.0	3.5	3.9	0.0412

WATER

	d.f.	s.s.	m.s.	F-value	PR>F
Model	8	58.421	7.3026	19.02	0.0001
Error	9	3.455	0.3838		
Corrected Total	17	61.876			

R-square=0.944 C.V.=1.37

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Treatment	2	31.548	15.823	41.22	0.0001
Position	2	22.174	11.087	28.88	0.0001
Treatment* Position	4	4.599	1.150	2.99	0.0792

TABLE 12

The effects of seed position and size on hours to 50% germination and water content at 50% germination in Neepawa wheat

HOURS

	d.f.	s.s.	m.s.	F-value	PR>F
Model	5	3024.28	604.86	44.36	0.0001
Error	18	245.41	13.63		
Corrected Total	23	3269.69			

R-square=0.925 C.V.=7.907

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	1	0.15	0.15	0.01	0.9175
Position	2	2993.48	1496.74	109.78	0.0001
Size*position	2	30.65	15.33	1.12	0.3468

WATER

	d.f.	s.s.	m.s.	F-value	PR>F
Model	5	230.03	46.01	7.34	0.0007
Error	18	112.81	6.27		
Corrected Total	23	342.84			

R-square=0.671 C.V.=4.456

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	1	56.734	56.734	9.05	0.0075
Position	2	169.623	84.812	13.53	0003
Size* Position	2	3.670	1.835	0.29	0.7497

TABLE 13

The effects of seed position and temperature on hours to 50% germination and water content at 50% germination in Neepawa wheat containing post-harvest dormancy.

HOURS

	d.f.	s.s.	m.s.	F-value	PR>F
Model	5	2111.74	422.35	84.62	0.0001
Error	6	29.95	4.99		
Corrected Total	11	2141.69			

R-square=0.986 C.V.=4.68

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temperature	1	243.90	243.90	48.87	0.0004
Position	2	1863.04	931.52	186.65	0.0001
Temperature* Position	2	4.80	2.40	0.48	0.6401

WATER

	d.f.	s.s.	m.s.	F-value	PR>F
Model	5	231.44	46.29	17.22	0.0017
Error	6	16.13	2.69		
Corrected Total	11	247.56			

R-square=0.935 C.V.=2.69

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temperature	1	88.02	88.02	32.75	0.0012
Position	2	139.63	69.82	25.98	0.0011
Temperature* Position	2	3.79	1.90	0.71	0.5307

TABLE 14

Effect of seed size and temperature on hours to 50% germination and water content at 50% germination using the temperature gradient plate.

HOURS

	d.f.	s.s.	m.s.	F-value	PR>F
Model	9	25528.94	2836.66	93.67	0.0001
Error	35	1059.86	30.28		
Corrected Total	44	26588.80			

R-square=0.960 C.V.=10.46

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	1	1499.66	1499.66	49.52	0.0001
Temperature	4	23832.58	5958.15	196.76	0.0001
Size*Temp	4	196.71	49.18	1.62	0.1901

WATER

	d.f.	s.s.	m.s.	F-value	PR>F
Model	9	402.16	44.685	9.44	0.0001
Error	35	156.61	4.732		
Corrected Total	44	567.78			

R-square=0.708 C.V.=3.66

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	1	0.3764	0.3764	0.08	0.7796
Temperature	4	378.2520	94.5630	19.98	0.0001
Size*Temp.	4	23.5351	5.8838	1.24	0.3106

TABLE 15

Neepawa R-square values

			Medium Light		Medium Dense		Large	
			Germination	Water Content	Germination	Water Content	Germination	Water Content
8 C	3ml	1	0.856	0.026	0.619	0.394	0.989	0.917
		2	0.852	0.145	0.684	0.545	0.914	0.371
	10ml	1	0.700	0.359	0.504	0.652	0.905	0.789
		2	0.765	0.206	0.603	0.186	0.912	0.621
12 C	3ml	1	0.875	0.567	0.846	0.687	0.873	0.674
		2	0.771	0.917	0.917	0.682	0.838	0.285
	10ml	1	0.827	0.695	0.857	0.753	0.793	0.668
		2	0.810	0.805	0.884	0.806	0.887	0.630
15 C	3ml	1	0.669	0.878	0.845	0.689	0.924	0.741
		2	0.456	0.896	0.797	0.844	0.753	0.915
	10ml	1	0.412	0.815	0.884	0.920	0.927	0.991
		2	0.386	0.689	0.851	0.874	0.855	0.916
23 C	3ml	1	0.950	0.924	0.986	0.935	0.925	0.351
		2	0.961	0.857	0.990	0.863	0.944	0.971
	10ml	1	0.986	0.941	0.972	0.953	0.953	0.730
		2	0.958	0.957	0.931	0.904	0.886	0.994

TABLE 16

Norstar R-square values

			Germination	Water Content
8 C	3ml	1	0.712	0.702
		2	0.800	0.647
	10ml	1	0.876	0.625
		2	0.921	0.882
12 C	3ml	1	0.863	0.776
		2	0.918	0.743
	10ml	1	0.817	0.807
		2	0.922	0.753
15 C	3ml	1	0.873	0.784
		2	0.846	0.771
	10ml	1	0.905	0.914
		2	0.958	0.691
23 C	3ml	1	0.922	0.636
		2	0.994	0.734
	10ml	1	0.817	0.703
		2	0.763	0.781

TABLE 17

The effect of seed size, temperature, and sand water on the lag time in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	24947.11	1084.66	373.08	0.0001
Error	24	69.77	2.91		
Corrected Total	47	25016.88			

R-square=0.997 C.V.=3.367

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	1968.77	984.39	338.59	0.0001
Temp	3	22374.57	7458.19	2565.36	0.0001
Size*Temp	6	532.71	88.79	30.54	0.0001
Water	1	47.76	47.76	16.43	0.0005
Size*Water	2	11.83	5.92	2.03	0.1527
Temp*Water	3	0.96	0.32	0.11	0.9535
Size*Temp* Water	6	10.51	1.75	0.60	0.7257

TABLE 18

The effect of seed size, temperature, and sand water on the post-lag germination rate in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	5.3677	0.2334	33.36	0.0001
Error	24	0.1679	0.0070		
Corrected Total	47	5.5356			
	R-square=0.9697		C.V.=10.847		

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	0.27036	0.13518	19.32	0.0001
Temp	3	2.45327	0.81776	116.90	0.0001
Size*Temp	6	2.41166	0.40194	57.46	0.0001
Water	1	0.00008	0.00008	0.01	0.9157
Size*Water	2	0.04463	0.02232	3.19	0.0591
Temp*Water	3	0.11535	0.03845	5.50	0.0051
Size*Temp* Water	6	0.07237	0.01206	1.72	0.1585

TABLE 19

The effect of seed size, temperature, and sand water on the hours to 50% germination in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	39985.63	1738.51	1114.21	0.0001
Error	24	37.45	1.56		
Corrected Total	47	40023.07			

R-square=0.999 C.V.=1.802

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	3694.97	1847.49	1184.06	0.0001
Temp	3	34562.96	11520.99	7383.83	0.0001
Size*Temp	6	1580.00	263.33	168.77	0.0001
Water	1	118.57	118.57	75.99	0.0001
Size*Water	2	0.52	0.26	0.17	0.8487
Temp*Water	3	20.70	6.90	4.42	0.0130
Size*Temp* Water	6	7.92	1.32	0.85	0.5476

TABLE 20

The effect of seed size, temperature, and sand water on the water content at the end of the lag period in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	480.021	20.870	21.84	0.0001
Error	24	22.940	0.956		
Corrected Total	47	502.960			

R-square=0.9547 C.V.=1.822

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	18.437	9.229	9.65	0.0008
Temp	3	392.311	130.437	136.47	0.0001
Size*Temp	6	54.501	9.084	9.50	0.0001
Water	1	1.837	1.837	1.92	0.1784
Size*Water	2	0.787	0.394	0.41	0.6672
Temp*Water	3	5.402	1.801	1.88	0.1593
Size*Temp* Water	6	7.725	1.288	1.35	0.2756

TABLE 21

The effect of seed size, temperature, and sand water on the post-lag water uptake rate in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	1.86012	0.08087	15.20	0.0001
Error	24	0.12771	0.00532		
Corrected Total	47	1.98782			

R-square=0.93576 C.V.=20.722

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	0.11416	0.05708	10.73	0.0005
Temp	3	1.53856	0.51285	96.38	0.0001
Size*Temp	6	0.17223	0.02871	5.39	0.0012
Water	1	0.02104	0.02104	3.95	0.0583
Size*Water	2	0.00208	0.00104	0.20	0.8235
Temp*Water	3	0.00639	0.00213	0.40	0.7539
Size*Temp* Water	6	0.00565	0.00094	0.18	0.9805

TABLE 22

The effect of seed size, temperature, and water content on the water content at 50% germination in Neepawa wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	23	203.42	8.8436	11.37	0.0001
Error	24	18.667	0.7778		
Corrected Total	47	222.069			

R-square=0.9159 C.V.=1.4996

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Size	2	7.310	3.655	4.70	0.0190
Temp	3	154.682	51.561	66.29	0.0001
Size*Temp	6	27.878	4.656	5.97	0.0006
Water	1	7.153	7.153	9.20	0.0058
Size*Water	2	0.457	0.229	0.29	0.7482
Temp*Water	3	4.220	1.407	1.81	0.1726
Size*Temp* Water	6	1.702	0.284	0.36	0.8940

TABLE 23

The effect of temperature and sand water on the lag-time in Norstar wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	3702.52	528.93	165.67	0.0001
Error	8	25.54	3.19		
Corrected Total	15	3728.06			
	R-square=0.993		C.V.=4.89		

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	3682.16	1227.39	384.44	0.0001
Water	1	18.49	18.49	5.79	0.0427
Temp*Water	3	1.87	0.62	0.20	0.8966

TABLE 24

The effect of temperature and sand water
on the post-lag rate of germination in Norstar wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	0.19530	0.02790	10.13	0.0020
Error	8	0.02203	0.00275		
Corrected Total	15	0.21732			

R-square=0.899 C.V.=10.327

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	0.1896	0.0632	22.96	0.0003
Water	1	0.0049	0.0049	1.80	0.2168
Temp*Water	3	0.0007	0.0002	0.09	0.9647

TABLE 25

The effect of temperature and sand water on the hours to 50% germination in Norstar wheat.

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	4749.10	678.44	824.02	0.0001
Error	8	6.59	0.82		
Corrected Total	15	4755.69			
	R-square=0.999		C.V.=1.84		

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	4741.95	1580.65	1919.82	0.0001
Water	1	6.36	6.36	7.73	0.0239
Temp*Water	3	0.79	0.27	0.32	0.8098

TABLE 26

The effect of temperature and sand water on the end of lag-water content in Norstar wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	146.05	20.86	19.80	0.0002
Error	8	8.43	1.05		
Corrected Total	15	154.48			

R-square=0.945 C.V.=2.462

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	137.05	45.68	43.36	0.0001
Water	1	6.08	6.08	5.77	0.0431
Temp*Water	3	2.93	0.98	0.93	0.4710

TABLE 27

The effect of temperature and sand water on the post-lag water uptake rate in Norstar wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	0.2880	0.0411	9.82	0.0022
Error	8	0.0335	0.0042		
Corrected Total	15	0.3215			

R-square=0.982 C.V.=19.88

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	0.2669	0.0890	21.23	0.0004
Water	1	0.0107	0.0107	2.54	0.1494
Temp*Water	3	0.0105	0.0035	0.83	0.5121

TABLE 28

The effect of temperature and sand water on the water content at 50% germination in Norstar wheat

	d.f.	s.s.	m.s.	F-value	PR>F
Model	7	83.107	11.872	65.96	0.0001
Error	8	1.440	0.180		
Corrected Total	15	84.547			

R-square=0.983 C.V.=0.929

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Temp	3	81.319	27.106	150.60	0.0001
Water	1	0.525	0.525	3.25	0.1090
Temp*Water	3	1.203	0.401	2.23	0.1624

TABLE 29

The effect of number of seeds per cage
on vapour phase water uptake

	d.f.	s.s.	m.s.	F-value	PR>F
Model	5	16310.2	3262.044	1519.18	0.0001
Error	183	392.9	2.147		
Corrected Total	188	16703.2			
	R-square=0.976		C.V.=4.02		

Anova

	d.f.	s.s.	m.s.	F-value	PR>F
Density	1	149.47	149.47	69.61	0.0001
Hours (Density)	2	12257.75	6128.88	2854.31	0.0001
Root Hours (Density)	2	3903.00	1951.50	908.84	0.0001

Appendix B

FIGURES

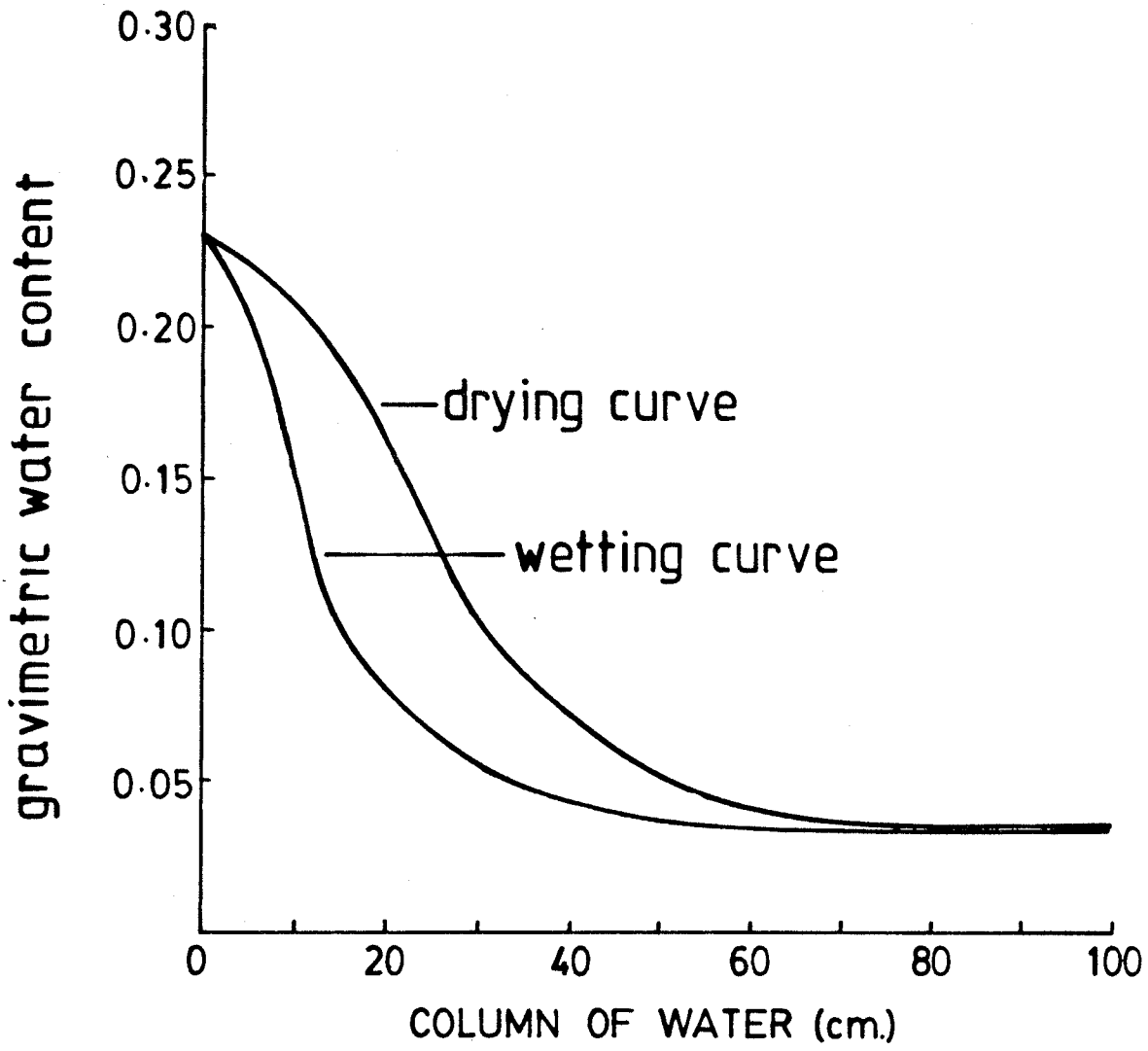


Fig. 43 The water potential water content relationship of Fisher Scientific 85-125 mesh fine silica sand.