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THE UNIVERSITY OF ALBERTA

The Root System of Canada Thistle (*Cirsium arvense* (L.)Scop.): Nitrogen Effects on Root Bud Dormancy

by

Léonie B. Nadeau

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **The Root System of Canada Thistle (*Cirsium arvense* (L.)Scop.): Nitrogen Effects on Root Bud Dormancy** submitted by Léonie B. Nádeau in partial fulfilment of the requirements of the degree of Doctor of Philosophy in Weed Science.

Supervisor

Date April 26 19 88

ABSTRACT

The root system of Canada thistle reached a depth of about 1.5 m in 1-year old stands, and of about 2 m in 2- and 10-year old stands. A quarter to a third of the total root length and root dry matter, and half of the total root bud production, were in the top 20 cm of soil. Root fragments sampled at all depths were able to produce new shoots, independent of the presence of root buds. The rate of linear expansion of the root system was estimated using ^{15}N, and approximated 1 cm per day for plants up to 13 weeks old.

Canada thistle was exposed to two nitrogen levels in nutrient solution and in soil. Under growth room conditions, the effects of nitrogen on root bud dormancy were influenced by light intensity and possibly by root carbohydrate levels. Under field conditions, the response of Canada thistle plants grown for 7 or 13 weeks in large containers filled with soil appeared to be influenced more by temperature regimes and precipitation levels than by nitrogen fertilization. However, in 1- and 2-year old stands and in 11- and 12-year old stands, nitrogen fertilization increased shoot production. In 1-and 2-year old stands, the increase in shoot production was associated mainly with an increase in root length and root biomass in the top 20 cm of soil and not with a release of root bud dormancy. The Canada thistle problem in nitrogen-fertilized stands could be more severe than in untreated stands. Cultivation of nitrogen-fertilized stands could result in more roots being spread throughout the field than in the case of untreated stands.

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1. INTRODUCTION

Canada thistle (*Cirsium arvense* (L.) Scop.) is a native of Europe, Western Asia, and North Africa, and probably found its way to eastern North America early in the 17th century as a contaminant of farm seeds (Detmers, 1927). Since its introduction, Canada thistle has spread throughout the United States and Canada as far north as 59°N (Moore, 1975) and is now one of the most common perennial weeds in the Prairie provinces, with at least 9 million ha of cultivated land infested (Hunter, 1973). In Alberta, 35% of all cultivated fields have an infestation level of at least five Canada thistle shoots per square meter (Thomas, 1980).

Why did Canada thistle become such a problem? The thistle is a deeprooted perennial weed that spreads vegetatively by an extensive root system and forms new shoots from root buds. Its resistance to eradication can be attributed to its capacity for vegetative reproduction from the many buds produced on the roots (Hunter, 1973). The importance of this weedy character is increased by the ability of the roots to survive adverse conditions and regenerate from small fragments as short as 6 mm (Forsberg, 1962). Furthermore, upright subterranean shoots can produce buds at any node and roots at any place, and both horizontal and vertical roots can form buds and roots at any point.

Cultural control of Canada thistle has been practiced and recommended for a number of years on summerfallow by the use of tillage or mowing (Arny, 1932; Cox, 1913; Detmers, 1927; Welton et al., 1929). Cultivation practices are aimed mainly at starving the thistle roots by repeatedly destroying new shoots. Variations of the depletion process have been recommended, but the general principle is to time cultivation to assure continuous depletion of root reserves.

Our present farming practice of continuous cropping has increased the importance of herbicide use as a control measure, and because of the persistence of the root system it is necessary that a herbicide be capable of being translocated into the root system and root buds. When the plant is growing undisturbed, root buds are relatively inactive, their growth being arrested by the inhibiting influence of the root apex and parent shoot (Parker, 1976). Releasing the lateral buds from inhibition would increase the sink size for translocation and therefore should increase the efficacy of foliage-applied herbicides (Hunter and McIntyre, 1974; Hunter and Smith, 1972; McIntyre and Hsiao, 1982; Parker, 1976; Regimbal and Martin, 1985).

The factors that affect the initiation and growth of root buds have received relatively little attention. The mechanism of apical dominance is still the subject of considerable controversy (Phillips, 1975). Root buds may fail to grow because of an excess of growth inhibitors such as auxins or because of a shortage of essential materials such as growth promotors (Thind, 1975), mineral nutrients (Hamdoun, 1970; McIntyre, 1965, 1972; McIntyre and Hunter, 1975), sugars (Parker, 1976), or even water (Hsiao and McIntyre, 1984; Hunter et al., 1985).

Investigations with quackgrass (*Agropyron repens* (L.)Beauv.) (McIntyre, 1965), leafy spurge (*Euphorbia esula* L.) (McIntyre, 1972; Regimbal and Martin, 1985) and Canada thistle (McIntyre and Hunter, 1975) have shown that buds on the roots or rhizomes can be released from inhibition and induced to develop into leafy shoots by increasing the nitrogen supply. In quackgrass, dormancy of rhizome buds was shown to be associated with very low internal nitrogen levels (Buchholtz, 1962; Leakey, 1974).

The effects of nitrogen on root systems have been demonstrated using young plants under controlled conditions, most often in nutrient solutions. If similar effects could be observed under field conditions for Canada thistle plants of different ages, then it might be expected that nitrogen treatments could increase the efficacy of herbicides.

The effects of supplementary nitrogen were studied first by growing Canada thistle in nutrient solutions of one of two nitrogen levels, and later with plants in soil in large containers in the greenhouse or in the field, and with planted stands in field plots. To minimize the variability, the effects of nitrogen on root bud dormancy were studied on a single clone of Canada thistle. Since Canada thistle spreads mainly by root fragments, all the Canada thistle plants studied were grown from buds on root fragments.

In Alberta, no descriptive study of the root system of an established stand of Canada thistle has been carried out. It was necessary to obtain information on the distribution of roots and root buds of Canada thistle and on the ability of these buds to produce shoots, before designing experiments in which the response of the root system to nitrogen would be studied at various growth stages. To obtain such information, an established stand of Canada thistle was excavated, and the rate of expansion of root systems was estimated using ^{15}N as a tracer.

Thus, the objectives of this project were 1) to describe the root system of Canada thistle under field conditions found in Alberta and 2) to examine the effect of supplementary nitrogen on root bud dormancy.

2. LITERATURE REVIEW

2.1 Canada Thistle Phenology

The morphology of Canada thistle leaves and flowers varies greatly within ecotype, to the extent that Detmers (1927) commented on the remarkable variation in growth of seedlings from one parent. In addition, high phenological variation has been observed (Hodgson, 1968). It has been proposed that the evolution of some plant species favored phenotypic plasticity rather than heterozygosity, assuring the survival of that species (Schlichting, 1986). This trade-off defines well the survival mechanism of Canada thistle, since its vegetative reproduction is far more prevalent than its reproduction through seeds. The ecotype most commonly found in western Canada has rough, spiny, wrinkled leaves, while the second most common ecotype has less spiny and rather smooth leaves (Alberta Agriculture, 1984).

In Alberta, Canada thistle shoots generally emerge in mid-May and show most rapid growth in June. Flowering occurs from mid-June to September. New shoots will continue to emerge into July in open sites (Alberta Agriculture, 1984). Even after frost, Canada thistle may continue to produce new shoots (Rogers, 1929).

Seedlings become established in recently plowed or disturbed soil, but are capable of germinating in uncultivated ground (Hodgson, 1968). New seedlings become established slowly and are sensitive to shading or competition (Bakker, 1960; Detmers, 1927). Poorly aerated soils or soils prone to drought are unfavorable for Canada thistle growth (Bakker, 1960; Hodgson, 1968), even though Rogers (1928) observed that thistle plants could survive in dry areas but did not flower when the soil was maintained at 30 or 60% of field capacity. Hodgson (1968) stated that rainfall of 400 to 750 mm per year was favorable for thistle growth. Amor and Harris (1974) noted that the heaviest infestation in Australia occurred in areas with 700 to 1000 mm mean annual rainfall.

After emergence, shoots develop rosettes and, if the photoperiod is longer than 16 hours, shoots grow rapidly within 3 weeks after emergence. The most rapid elongation reported was 3 cm/day, and corresponded to the period when root reserves were lowest (Hodgson, 1968).

Hodgson (1968) stated that emergence of shoots began when the average weekly air temperature was above 5°C and was greatest at a mean temperature of 8°C, but varied with ecotype. Growth was greater at a 25/15°C day/night temperature regime, under controlled conditions, than at a 15/5°C or a 30/22°C day/night temperature regime (Hoefer, 1981; McAllister and Haderlie, 1985b). A root temperature of 17°C resulted in plants with greater dry weights at the above noted air temperature and photoperiod regimes than when root temperature was allowed to fluctuate with air temperature (Hoefer, 1981). Hunter and Smith (1972) found both root/shoot ratio and number of root buds emerging through the root cortex to be inversely related to temperature (ranging from 16 to 27°C) and length of photoperiod (ranging from 12 to 16 hours). McAllister and Haderlie (1985b) noticed that very strong interactions between temperature and photoperiod existed, with environmental conditions approaching fall conditions in Nebraska favoring root bud initiation, and an environment simulating summer conditions favoring shoot growth.

A nutrient solution with a very low nitrogen level (around 5 ppm) was sufficient for growth (Hamdoun, 1970; Wilson, 1979). Optimum levels of nitrogen were between 50 and 150 ppm, with very high levels detrimental to growth. Shoot dry weight, shoot/root ratio, and root bud growth were generally higher with higher nitrogen levels (Hamdoun, 1970; Hoefer, 1981; McIntyre and Hunter, 1975). Wilson (1979) stated that Canada thistle was tolerant of high salt concentration and that growth could occur with soil salt content of up to 2%.

2.2 Propagation

The importance of seeds in the establishment of new Canada thistle infestations is uncertain. Chancellor (1970) studied the establishment of Canada thistle in a field with several plants along its fence line and recorded only 13 seedlings after 7 years. The importance of seed in survival and spread of the species is as doubtful in Canada thistle as in other perennial weedy species, such as poverty weed (*Iva axillaris* Pursh) (Best, 1977) and quackgrass (Werner and Rioux, 1977).

Vegetative reproduction may be summarized as occurring in two ways: 1) the underground shoots are able to produce buds at any node and roots at any point and 2) horizontal and upright roots can produce shoots or roots at any place (Hunter, 1973).

In the following sections, root buds will refer to buds giving rise to shoots, and root primordia to buds giving rise to lateral roots. Emerged root buds will refer to root buds that have emerged through the root cortex.

Canada thistle is able to regenerate top growth very early in its life cycle. Wilson (1979) found that 8% of 19-day old plants regenerated top growth after clipping. Emerged root buds were observed on roots as early as 3 weeks after shoot emergence in a nutrient solution medium (Hoefer, 1981). At 40 days, two to three shoots sometimes appeared after clipping (Wilson, 1979). Two months after seedling emergence. Hunter (1973) counted 39 emerged root buds. Detmers (1927) found 19 emerged root buds on roots of a 4-month old greenhouse-grown plant.

Vegetative spread through horizontal extension of the root system can be rapid if competition is low. Bakker (1960) observed extensions of 4 to 5 m in one season, while Hayden (1934) observed extensions of 6 m. A root section planted at Lincoln, Nebraska, covered 113 m^2 within 2 years (Hoefer, 1981). Chancellor (1970) reported that in Saskatchewan, an infestation established by a root fragment could extend 4 m in the first year and 12 m in subsequent years. The spread of Canada thistle is comparable to that of other perennial weeds, such as poverty weed (Pavlychenko, 1943).

Rogers (1929), Coukell (1966), Haderlie and McAllister (1981) and McAllister and Haderlie (1985a) noted that in Iowa, Manitoba, and Nebraska, respectively, Canada thistle root systems still showed some root bud activity in winter. Rogers (1929), for example, reported that root buds grew into shoots as long as the growing season was warm. When the shoots that had emerged from the soil were killed by frost in autumn, new shoots were still developing in the unfrozen ground. These shoots were delicate and slender, and were killed quickly by the freezing of the ground. In early January, the latent buds on the larger roots were larger than those observed 3 weeks earlier. Soil had been frozen since the middle of December, and ice crystals were present at the point of attachment of the buds.

Pavlychenko (1943) stated that, in the case of drought, Canada thistle shoots from a patch would quickly dissociate themselves from the mother plant and would live independently at the expense of food and water stored previously. He explained that, in this manner, the plant appears to abandon old patches where moisture is depleted. However, allelopathic chemicals could also play a role (Bendall, 1975).

The root has the ability to regenerate from pieces as short as 6 mm

(Forsberg, 1962). Root diameter is of some importance in determining its ability to produce shoots, but is more important in determining the size of the new shoots (Hamdoun, 1972). Forsberg (1962) observed that when root sections of various length were planted in vermiculite, root sections 6 mm long could produce two shoots and one root. When the shoots and roots were removed weekly, the root fragments required 164 days to decay. Similarly, 10-cm root sections produced 15 shoots and 24 roots and needed 226 days to decay. Creeping horizontal roots produced shoots more readily than vertical roots (Chancellor, 1970). As the earliest shoots appeared within 5 days of fragmentation, the buds probably were preformed (Hunter, 1973). The ability of lateral roots to produce shoots was greatest in spring and fall and least in the summer months.

Forsberg (1962) noticed an increasing number of shoots or roots produced per centimeter of root as root fragments were shorter. He suggested that a reduced amount of inhibitor or reduced competition for nutrients may have resulted in increasing the initiation and growth of shoots and roots.

2.3 Root Distribution

Forsberg (1962) found that 4 to 5 weeks after germination under field conditions, secondary roots emerged on the main vertical root. Ten to 11 weeks after emergence, new aboveground shoots were produced from the lateral roots. The average length of a lateral root at this time was 104 cm and the main root extended to a depth of 81 cm. The developing tap-fibrous root system was reported to vary considerably (Hayden, 1934). A seedling with two leaves might have a simple branching root system 3 to 15 cm long.

Occurrence of roots down to 2 to 3 m is common (Hunter, 1985; Pavlychenko, 1943). These depths are comparable to the ones observed by Pavlychenko (1943) for poverty weed. Hayden (1934) observed that the depth of penetration depended on the depth of the water table.

Fibrous roots are generally found in the upper soil layer, where the root system is frequently cut by tillage equipment (Hunter, 1973). In a study done by Forsberg (1962), the majority of the dry weight of the root system was located between 30 and 90 cm depth. Hodgson (1968) found that 54% of the dry weight of the root system of a young Canada thistle infestation was in the 7.5 to 23-cm soil layer, while 30% was between 23 and 38 cm and 16% between 38 and 54 cm. In an established infestation, Hunter (1985) observed 41% of the root weight between 60 and 90 cm. Underground shoots generally did not arise from below 30 cm (Hayden, 1934).

Hayden (1934) excavated a thistle patch in a loam soil in Iowa which was seeded to corn. Trenches were 2 m wide, 3 m long, and 3 m deep. The upper 15 cm was cultivated early in the season but at the time of the excavation had become a hardpan. She observed that some of the shoots that broke through the crust were coiled and, for about 1.5 m below the crust, the soil was penetrated by numerous vertical and horizontal roots. At depths of up to 1 m, horizontal roots grew out from the vertical roots and bore many stems and emerged root buds. The horizontal roots arched upward or downward and often terminated in fine branches. The horizontal roots bore few secondary branches, while the vertical roots bore many branches. The vertically descending roots terminated in clay at the water table at 2 to 2.3 m.

Pavlychenko (1943) observed two types of roots in Canada thistle which illustrated their ecological adaptation to the environment. The first category was produced from underground stem tissue or root tissue 30 cm from the surface. The roots grew horizontally for short distances and then turned downward to produce vertical roots. New shoots arose at the bending point. The second kind originated from stem tissue; they were located between the soil surface and 30 cm depth. These roots quickly invaded new areas. No other authors used Pavlychenko's classification, probably because of the lack of a distinct difference between the two root types in the field.

Pavlychenko (1943) classified Canada thistle with a group of weeds having deep, profusely branched tap roots. The tap roots and their branches were thick structures supplied with carbohydrate reserves, and capable of developing meristematic centres almost at any point over their length. He stated that poverty weed, hoary cress (*Cardaria draba* (L.)Desv.), field bindweed (*Convolvulus arvensis* L.), Russian knapweed (*Centauria repens* L.), and leafy spurge belonged to this class.

2.4 Root and Root Bud Anatomy

Canada thistle has a complex underground system of shoots and roots. Hamdoun (1970) superficially classified three types of structures: short fine roots, long and thick horizontal and vertical roots; and vertical parts of stems.

The young roots are mostly diarch or triarch (Thind, 1975), even though Hamdoun (1967) observed that herbicides could bring about changes in the anatomy of roots of Canada thistle. All root primordia and root buds originated from the pericycle. Root buds originate from the protoxylem poles, and exhibit negative geotropism. The origin of root buds in Canada thistle is very similar to that of milkweed (*Asclepias syriaca* L.) (Polowick and Raju, 1982), but it differs from that of common toadflax (*Linaria vulgaris* Mill.), which is exogenous (Charlton, 1965).

The thick roots were reported to have a well developed cortex and phloem. The cortex and epidermis were retained during secondary thickening and the epidermis became impregnated with suberin (Detmers, 1932; Hamdoun, 1970). The reserve food material was stored in the form of soluble polysaccharides in sufficient amount to enable the root to survive long periods of adverse conditions (Arny, 1932; Welton et al., 1970).

McIntyre and Hunter (1975) observed that root buds were produced in close association with lateral roots or their scars. However, Thind (1975) observed that root buds can differentiate singly in the obtuse angle of lateral roots, with one primordium in the obtuse angle and one in the acute angle, at the base of an already existing root bud, or anywhere on the root system irrespective of the presence of a lateral root or scar. The differentiation of root buds of Canada thistle is similar to some other perennial weeds, such as milkweed and field bindweed but differs from others, such as common toadflax (Polowick and Raju, 1982).

At early stages of development, it is difficult to predict the fate of initials as they can give rise to a root bud or a root primordium. In the majority of cases, initials of Canada thistle that differentiate into root buds do so earlier than initials differentiating into root primordia (Thind, 1975). Root buds of Canada thistle (Thind, 1975), and of leafy spurge and milkweed (Polowick and Raju, 1982), quickly develop the ring of separate vascular bundles around the perimeter that is characteristic of dicotyledon stem tissue. Thind (1975) observed that the shoot apex of non-emerged buds of Canada thistle was already well-defined, with its leaf primordia comprising 12 to 14 leaves. The shoot apex was seen as a large protuberance on the surface of intact roots as compared to the relatively small cone-shaped structure of root primordia. Sometimes a cavity appeared above the developing bud, which was probably due to the crushing of cortical cells as the bud forced its way through the cortex.

The apex of non-emerged root buds produced a number of leaf primordia. The first leaves, which provided protection for the apex when the shoots penetrated the soil, remained as simple scale leaves (Hamdoun, 1970). The underground stems arose from the root buds and could bear fibrous roots that originated in the interfascicular cambium.

2.5 Root Bud Dormancy

Dormancy is the inability of viable reproductive structures of plants to grow when the immediate environmental conditions are favorable for growth. The ecological advantage of the strategy is the ability to avoid the commitment of resources to active growth when the prospects are poor for completion of the life cycle or for replenishment of organic reserves. Innate dormancy, correlative inhibition, and quiescence are often used to describe root bud dormancy. Innate dormanc[illegible]ld occur "within buds" (Nissen and Foley, 1987). Correlative inhibition, sometimes called induced dormancy, can apply to root buds if their growth is inhibited by an endogenous mechanism induced by external influences (McAllister and Haderlie, 1981). Quiescence, which is used inaccurately to describe dormancy, implies that development and growth are inhibited by environmental influences.

Bud dormancy is the main source of difficulty in killing perennial weeds. Roots fail to translocate herbicides to inactive root buds, and thus the inactive buds can be the source of new growth. Extra sprouting during, slightly before or slightly after the time of herbicide application would increase sink size and herbicide translocation and thus the degree of weed control (Parker, 1976).

The need to distinguish between cause and effect is the main difficulty in assessing the role of internal factors in the mechanisms of apical dominance.

2.5.1 Growth Regulators

Innate dormancy was observed in Canada thistle (Martin, 1971) and in leafy spurge (Nissen and Foley, 1987). Canada thistle root fragments sampled monthly for levels of gibberellins and abscisic acid showed seasonal variations, with gibberellins high in summer months and abscisic acid high in winter months (Thind, 1975). Martin (1971) stated that the effect of shoot removal on thistle root bud dormancy depended on the time of removal. In Ohio, he observed that shoot removal stimulated root bud activity in March but not in May. Innate dormancy is not well understood, especially in Canada thistle. Root bud dormancy of Canada thistle is better defined by correlative inhibition.

Interference with apical dominance and release of root bud dormancy was observed by low doses of herbicides as in the cases of glyphosate (*N*-(phosphonomethyl)glycine) on leafy spurge (Maxwell et al., 1987) and chlorsulfuron (2-chloro-*N*-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzenesulfonamide) on Canada thistle (Donald, 1986). Usually, the effect on bud dormancy is the result of damage to the mother shoot. Once the apex is destroyed, no correlative inhibition exists.

Several theories have been put forward to explain correlative inhibition. A plant growth regulator theory, which describes the interaction of auxins and cytokinins, is favored by Phillips (1975). Auxins produced in the apical meristem are transported basipetally. The accumulation of auxins in roots would inhibit the initiation and growth of new shoots (Eliasson, 1961). Cytokinins are produced in growing root tips and transported upward. They would stimulate the production of initials and the release of root bud dormancy. With apical meristem removal, the concentration of auxins in the roots decreases while the concentration of cytokinins increases and the release of root bud dormancy is facilitated. Schier (1981) suggested that in aspen (*Populus* spp.), auxins maintain apical dominance by promoting the degradation of cytokinins. Schier (1981) believed that cytokinins might exert their role only if the auxin/cytokinin ratio fell below a certain level.

Other hormonal factors may influence bud dormancy. In Canada thistle, ethephon (2-chloroethyl phosphonic acid) and auxin applied to root fragments inhibited the production of root buds but had no effect on shoot elongation (Martin, 1970). Carson (1974), who sprayed ethephon on intact Canada thistle plants grown under controlled conditions, noticed an increase in the production of shoots compared to controls. He suggested that ethylene released upon degradation of ethephon may have activated the dormant root buds and altered the sink-source distribution of the plant. As a result, increased basipetal movement of herbicides occurred. Carson observed that the shoots produced after ethephon treatment were morphologically different from the shoots produced in untreated plants, having narrow leaves without spines instead of the normal spiny leaves.

In Martin's study (1971), gibberellins applied to roots of Canada thistle had no effect on root production or shoot elongation. Thind (1975), however, observed that root-applied gibberrellins stimulated emerged root bud production and elongation of Canada thistle shoots. Schier (1981) stated that the effect of gibberellins on suckering from excised roots in aspen depended on the stage of development of the root buds when the roots were excised and treated. If root buds arose from newly initiated meristems, gibberellins would reduce sucker production because they would inhibit initiation and production of the first shoot primordia cells. As primordia increased in cell number, gibberellins showed progressively less inhibition of bud formation. At some stage in bud development, the inhibition changed to a stimulation of emergence of established root primordia.

Abscisic acid is a well-known growth inhibitor. Thind (1975) reported that abscisic acid applied to roots of Canada thistle inhibited both root bud production and growth. Similarly, Schier (1981) reported that root cuttings of aspen treated with abscisic acid did not produce any suckers.

Some scientists do not explain apical dominance solely by using plant growth regulators. Farmer (1962), for example, stated that isolation of roots from parent shoots not only might cut off the supply of bud growth inhibitors but that it was also conceivable that water and nutrients normally translocated to parent shoots would accumulate in isolated roots and result in the stimulation of root bud activity. Later, Hall and Hillman (1977) failed to detect exogenous tritiated auxins in buds when applied to decapitated shoots of beans (*Phaseolus* spp.), and in another experiment, Hillman et al. (1977) failed to detect any endogenous levels of auxins in buds of intact plants of beans. Therefore, Hillman et al. (1977) concluded that there must be some indirect effect resulting from the behaviour of auxins or their products at the site of application.

2.5.2 Temperature and Photoperiod

Many researchers concluded that root bud activity was greatest at 15°C (Hamdoun, 1972; Hoefer, 1981; Hunter and Smith, 1972; Thind, 1975), irrespective of photoperiod. When root pieces were incubated for 2 weeks at 15°C, more emerged and non-emerged root buds were detected than on comparable roots that were left at "room temperature" (McAllister and Haderlie, 1981).

Interactions between air and root temperatures and photoperiod have been reported. MacAllister and Haderlie (1985b) observed that bud initiation was greatest with a 25/15°C day/night air temperature regime, a constant root temperature of 20°C, and a 13-hour photoperiod, compared to other combinations of air temperature regimes of 15/5°C, 25/15°C or 30/22°C, root temperatures of 10°C, 20°C, and 30°C and 13-hour and 15-hour photoperiod. The greatest proportion of dry matter translocated to root buds occurred under 15/5°C day/night air temperature, 20°C root temperature and 13-hour photoperiod. Therefore, the number of buds produced under conditions approaching a typical fall season in Alberta would be close to maximum. Bud elongation and dry weight accumulation in root buds was highest at 25/15°C day/night temperature, a constant root temperature of 30°C and a 15-hour photoperiod, which would be more typical of summer temperature in Alberta.

Hoefer (1981) reported that a 15/5°C day/night regime was very favorable to root bud production regardless of photoperiod in established Canada thistle. A 25/15°C regime, on the other hand, was greatest for bud production of seedlings grown in a sand-soil mixture under a 15-hour photoperiod, but not under a 13-hour photoperiod.

Carson (1974) grew Canada thistle seedlings and subjected them to 24/16°C or 16/11°C day/night temperature regime, at growth stages of 0 to 60 days, 60 to 105 days or 105 to 150 days. He observed no significant difference in number of emerged root buds between the different temperature regimes. He noted, however, that for the 0 to 60-day old plants more root buds were produced at a 24/16 °C day/night regime than at the 16/11 °C day/night regime, and that the opposite was true for the 105 to 150-day old plants. Carson (1974) suggested that low temperatures at a late stage of plant development might be conducive not only to reserve buildup in roots but also to the formation of root buds.

2.5.3 Moisture

McIntyre (1979) reported evidence of competition for water between shoots and root buds as a factor in the mechanism of root bud inhibition in leafy spurge, and Hsiao and McIntyre (1984) observed similar results in milkweed. Hall and Hillman (1975) showed that bud length of beans (*Phaseolus vulgaris* L.) increased markedly within 30 min of decapitation of the parent shoot. An increase in water potential would be the most probable explanation of such a rapid response.

Hunter et al. (1985) studied the effects of 50% and 100% relative humidity on Canada thistle growth. They provided evidence of increased shoot and root growth under high relative humidity compared to low relative humidity when the parent shoot was left intact or was removed. Furthermore, the number of secondary shoots produced was higher under high humidity than under low humidity 4 days after the onset of the experiment. After 7 days, the number of shoots produced under low humidity was the same as the number produced under high humidity. In spite of these effects on shoot and root growth, the growth of root buds at high relative humidity was not significantly greater than at low relative humidity. Hunter et al. (1985) suggested that the lack of effect was caused at least partly by the inability of the buds to compete with the shoots for nitrogen.

Carbohydrate levels might also interact with moisture availability to dictate root bud activity. Field conditions that favor vegetative growth, for example high moisture and high soil fertility, will also favor the depletion of carbohydrates. Drought conditions following the onset of vegetative reproduction may alter the translocation of photosynthates in the plant, limit the replenishment of carbohydrate reserves in roots and prevent bud initiation and growth. However, drought conditions were found to have no effect on translocation of picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid), dicamba (3,6-dichloro-2-methoxybenzoic acid) or glyphosate in Canada thistle and control of the weed was unaffected by the different moisture conditions (Lauridson et al., 1983).

2.5.4 Root Carbohydrates

Production of root buds and release of dormancy may depend on the reserve supplies of non-structural carbohydrates (Arny, 1932; McAllister and Haderlie, 1985a; Welton et al., 1929). Compounds such as glucose, fructose, dextrins, starch and inulin can be used to fuel growth and development (Hodgson, 1968; Welton et al., 1929). In experiments by Hayden (1934), cuttings taken from stems about a year old were densely filled with carbohydrates and, when planted, 95% of them produced shoots. When cuttings were taken from underground shoots at the end of the flowering season, when carbohydrate levels were low, only 5 to 10% produced shoots.

A number of attempts have been made to describe seasonal fluctuations in carbohydrate reserves of Canada thistle (Arny, 1932; Coukell, 1966; McAllister and Haderlie, 1985b; Otzen and Koridon, 1970; Rogers, 1928; Welton et al. 1929). Welton et al. (1929) and McAllister and Haderlie (1985b) studied dry matter and carbohydrates of root systems and found a gradual decrease of dry matter and carbohydrates during the early part of the growing season, with a minimum at the onset of flowering. Similar trends were observed for leafy spurge and perennial sowthistle (*Sonchus arvensis* L.) (Arny, 1932) and Dalmatian toadflax (*Linaria dalmatica* (L.)Mill.) (Robocker et al., 1972). Welton et al (1929) also observed that, when the shoots of the thistle plants were clipped, the carbohydrate levels of the roots reached their lowest levels after secondary shoots started emerging. Similar results were reported by Arny (1932) and Hayden (1934). Otzen and Koridon (1970) concluded that little more information was obtained by the time-consuming carbohydrate analyses than could be obtained from estimation of dry matter content. Similar conclusions were cited by Coukell (1966), who also stated that carbohydrate level was not correlated with thistle vigour when the later was estimated by size of shoots and density of stands.

2.5.5 Nitrogen

Apical dominance has been reported to be influenced by mineral nutrition (Aspinall, 1961; McIntyre, 1965, 1972; McIntyre and Hunter, 1975). Studies on quackgrass (Buchholtz, 1962; Leakey, 1974; McIntyre, 1965) and leafy spurge (McIntyre, 1972; Regimbal and Martin, 1985) showed a marked effect of nitrogen not only on apical dominance, but also on root bud initiation and growth. Peterson (1975) stated that root bud growth in hawkweed (*Hieracium florentinum* All.) was highly responsive to the external nitrogen supply. Wainwright et al. (1986) stated that nitrate increased bud growth and rooting of shoot cuttings of blackcurrant (*Ribes nigrum* L.).

In work done on Canada thistle, perennial sowthistle and leafy spurge by Arny (1932) and on Canada thistle by Welton et al. (1929), root nitrogen gradually declined over the growing season, with a minimum at the onset of flowering, coincident with the lowest root carbohydrate level and the lowest root dry weight of the growing season. These minima corresponded to the reduced ability of lateral roots to produce new shoots. Otzen and Koridon (1970) also observed that root nitrogen content changes were similar to those of root dry weights and carbohydrate levels, except that the lowest level of root nitrogen occurred a few days later than the lowest level of root carbohydrate.

Many conflicting reports on the effect of nitrogen on root bud dormancy in Canada thistle have been published. In experiments done by Carson (1974), 100 ppm nitrogen in the growth medium resulted in a higher shoot/root ratio than 10 ppm, but no significant effect was observed on the number of emerged root buds. Similarly, Hoefer (1981) reported that nitrogen levels ranging from 8 to 84 ppm in the form of nitrate or ammonia in nutrient solution or in soil did not consistently stimulate the production of emerged root buds (<5mm long) or underground shoots (>5 mm long). He stated however, that in established stands, the low nitrogen treatment produced more shoots than the high nitrogen treatment, but that the opposite was true in the case of seedlings. He then explained that nitrogen probably increased the competitive ability of the existing shoots.

Hamdoun's results (1970) were different from Carson's (1974) and Hoefer's (1981). He recorded data on the number of emerged root buds on seedlings and on plants grown from root cuttings grown at different nitrogen levels in nutrient solution. Increases in number of emerged root buds (<1 cm long), in number of underground shoots (>1 cm long) and in number of aerial shoots were observed with increasing external nitrate concentration of up to 70 ppm, especially in plants grown from root cuttings. However, no significant further increase was noted for nitrogen concentrations ranging from 70 ppm to 210 ppm.

McIntyre and Hunter (1975) were the first scientists to study the effect of added nitrogen on the number of non-emerged root buds. They observed that the number of non-emerged root buds markedly decreased as the nitrogen level increased from 5 to 420 ppm. Ammonium was observed to increase root bud production more than nitrate. No differences in the number of emerged buds (< 1 cm) or the number of underground shoots (>1 cm) were recorded, but the length of underground shoots increased as nitrogen levels increased. McIntyre and Hunter

(1975) also observed that when their plants were harvested at a later growth stage, the number of emerged root buds tended to decrease as the external nitrogen level increased.

Hoefer (1981) used some split applications of nitrogen in his treatments, and stated that Canada thistle responded more to initial nitrogen levels than to a second application of nitrogen. But, as with his previous experiments, nitrogen did not consistently release root buds from dormancy. McIntyre and Hunter (1975) also studied the effect of split applications of nitrogen on seedlings grown in nutrient solution. No differences in number of emerged buds or in underground shoots were observed between treatments, but the length of underground shoots increased as external nitrogen increased. Furthermore, the number of aerial shoots tripled when seedlings were grown at nitrogen levels increasing from 5 ppm in the first nitrogen application to 420 ppm in the second application, compared to seedlings grown under a constant 5 ppm nitrogen level.

No evidence was obtained from these investigations as to the nature of the mechanisms involved in root bud dormancy. The degree of root bud growth and underground shoot growth could be dependent upon the ability of the root buds to compete for nitrogen or carbohydrates. The growth of underground shoots may have diverted carbohydrates from the roots in amounts sufficient to limit root bud response.

3. MATERIALS AND METHODS

3.1 Plant Source and General Procedures

Root fragments used in all experiments were obtained from greenhouse-grown Canada thistle plants which had been grown previously from root pieces obtained at the University of Alberta Ellerslie Research Station. Peat pots 7.5 cm wide by 7 cm deep were filled with a sand:soil:peat mixture (1:1:1) and root pieces 5 cm long, 3 to 7 mm in diam were planted in these pots. Plants were grown from root fragments under greenhouse conditions, at a 20/15°C day/night temperature regime, 200 $\mu E.m^{-2}.sec^{-1}$ light intensity, with a 16 to 18-hour photoperiod. At the 5 to 6-leaf stage, or 5 weeks after planting, plants were collected and used for experimentation. Canada thistle plants used for outdoor experiments were hardened for 2 weeks by exposing them to field conditions from mid-May to early June.

Outdoor experiments were done on an orthic black chernozem, of the Navarre silty clay loam series. The indoor experiment using soil was done in Navarre clay loam (14% sand, 30% silt, 56% clay, 15% O.M., pH 6.0).

Soil nutrient levels and soil moisture potential were determined by taking at least four soil samples with a soil auger at each of four different depths at the University of Alberta Ellerslie Research Station site and the Edmonton Research Station site throughout the growing seasons of 1984, 1985, and 1986. Soil pH, P and K were determined at the beginning of each growing season. Soil inorganic nitrogen and total soil nitrogen were determined in spring 1984, and repeatedly in 1985 and

1986 at both sites. Total soil N and inorganic soil N were obtained by Kjehdahl analysis. Soil extractable P was extracted using NH_4F and H_2SO_4 (Medium-strength Bray solution) and the amount was measured by spectrometry. Soil K was extracted with NH_4OAc, and the amount present was determined by atomic absorbance. Soil pH was determined using a 1:2 soil water ratio and a pH meter. The methodology for N, P, K and pH determination is described in more detail in McKeague (1978). Soil gravimetric water content was measured repeatedly during the 1984, 1985, and 1986 growing seasons and, with the appropriate moisture retention curve, was used to determine the soil moisture tension. Precipitation, air relative humidity, and air temperature were obtained for the University of Alberta Ellerslie Research Station from a small weather station[1] situated 500 m from the Canada thistle stand at the Ellerslie Research Station, and for the Edmonton Research Station from a hygrothermograph[2] and a rain gauge. Soil bulk densities for the Ellerslie Research Station site and the Edmonton Research Station site were calculated using the paraffin clod method described by Blake (1965).

Underground shoots were defined as root buds that had emerged through the cortex and were at least 5 mm long. Emerged root buds were defined as visible buds that were less than 5 mm long. Non-emerged root buds are buds that had not emerged through the cortex and could be detected only after the roots were cleared, using the methodology described by McIntyre and Hunter (1975). Roots were immersed in 80% lactic acid for 3 to 6 days at 60°C, with thick roots sometimes needing 8 days. It was important not to leave the roots in the hot lactic acid after they had been adequately cleared since a long treatment reduced the opacity of the

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[1] CR21 Micrologger, Campbell Scientific Inc., Logan, Utah.

[2] Hygrothermograph, Belfort Instrument Co., Baltimore, Maryland.

root buds and the stele. A light microscope at 10X magnification was used to detect the buds.

Shoot production was determined by planting 10-cm long root pieces in a sand:soil:peat mixture (1:1:1) and counting shoots produced from those root pieces after 28 days. Dry weights were determined by placing plant parts in an oven at 60°C for 2 to 3 days. Plant total nitrogen was obtained by Kjeldahl analysis. The detailed methodology is described in Bremmer and Mulvaney (1982). Root samples used for the determination of dry weight and nitrogen, for the determination of shoot production after planting root fragments and for the determination of numbers of emerged and non-emerged root bud were all different. Root length was recorded on all samples unless otherwise stated.

3.2 Descriptive Study of The Root System

3.2.1 Root System of an Established Stand

In the summer of 1984, a 10-year old stand of Canada thistle was studied at the Ellerslie Research Station. The thistle shoots covering four 2-m wide by 4-m long areas were cut down to 15 cm above the soil surface, at the flowering stage, on the 5th of July, approximately 7 weeks after shoot emergence, and the total shoot dry weight was determined. These areas were then excavated to a depth of 2 m with a backhoe. The soil profile on one of the 4-m long sides of each trench was used for study. Three successive 10-cm thick vertical slices were examined in each trench (Figure 1). For each slice, a grid of 20 cm by 20 cm was engraved in the soil profile and excavation of the roots then started from the bottom of the profile. Excavation was done for a horizontal distance of 10 cm inside the soil profile and for a vertical distance of 2 m from the soil surface. Roots in bands of soil of 20 cm were excavated systematically from the bottom of the soil profile to the soil surface.

A screwdriver was used to carefully remove roots larger than 1 mm diam from the soil. Roots smaller than 1 mm diam seldom had root buds. Furthermore, they were very difficult to free from the clay.

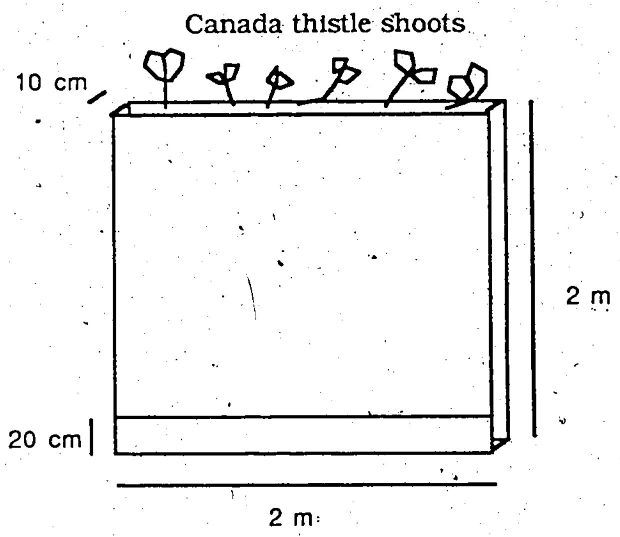

Figure 1. Description of the soil profile from which roots were excavated.

The lengths of all roots collected were measured for every 20 cm down the soil profile, and the number of underground shoots was recorded. Root oven-dry weight, root bud number, and shoot production were determined on the roots collected from the three slices of each trench, with root bud number determination, root dry weight, and shoot production of root fragments each measured on one of the three slices. Number of root buds and shoot production per meter of root were calculated. Roots from the first slice of each trench were always excavated as fast as possible and used for root bud determination since it had been reported that oxygen might affect root bud growth and initiation (McIntyre, 1979).

The length of time between root collection and the measurements was 1 to 2 days. Processing roots for root bud determination after 2 days resulted in more emerged root buds than for roots that were processed one day after collection. However, no differences in total number of root buds were observed within this time period. Therefore, no distinction between emerged and non-emerged root buds was made, and only total number of root buds are reported here.

Means and standard errors of the means were calculated for all measurements recorded.

3.2.2 Rate of Expansion of the Root System

Rate of expansion of the root sytem was determined using a non-destructive method to evaluate roughly the size of root systems of stands of different ages. In order to do so, the rate of expansion of the root system was studied using ^{15}N as a tracer. It was hypothesized that if roots reached a soil volume where ^{15}N is higher than its natural abundance, a high concentration of ^{15}N would be detected in the shoots supported by these roots. Ammonium ions were used as the source of ^{15}N. It was assumed that the low leaching characteristic of ammonium ions would improve the accuracy of the estimation of root expansion (Russel, 1978).

The natural abundance of ^{15}N is 0.36%, with variations around this value usually within the range 0.3564 - 0.3636% (Hauck and Bremmer, 1976). A source other than the natural abundance has to be involved if a level much higher than 0.36% ^{15}N is detected. It was arbitrarily decided that 0.40% was the minimum level required to be assured of the involvement of other ^{15}N sources. This corresponded to a 9.2% increase in ^{15}N over its natural abundance.

3.2.2.1 Preliminary ^{15}N Experiment

Canada thistle plants that were treated were in the rosette stage, with 6 leaves, and with no elongated stems. The solution of ^{15}N used was $^{15}NH_4Cl$[3] (19 mg/ml, 99% ^{15}N), containing 5 mg/ml ^{15}N. Sixteen plants were washed out of the peat pots in which they were grown and were planted in each of four 60 cm by 30 cm by 10 cm deep containers. One ml of ^{15}N solution was put at the surface of a root tip 10 cm away from the base of the plant, before the roots were covered with soil. Thistle plants were harvested 6, 12, 24 and 48 hours after ^{15}N was applied to the soil. One container containing four plants was harvested at each time. The plants were then divided into four parts:

1) three youngest leaves
2) three oldest leaves
3) the root in contact with ^{15}N
4) roots not in contact with ^{15}N

Corresponding parts of the four thistles in one flat were dried, then ground together in a Wiley mill[4] equipped with a 20-mesh grid. One sample of 400 to 500 mg was taken for each plant part at each sampling time, total nitrogen was determined using Kjeldahl analysis, and the ^{15}N abundance was measured with a mass spectrometer[5]. A detailed description of the methodology is provided by Bremner and Mulvaney (1982) and by Hauck (1982). A summary of the methodology is included in Appendix 1.

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[3] MSD Isotopes, Division of Merck Frosst Canada Inc., Montreal.

[4] Arthur H. Thomas Co., Philadelphia

[5] Ug Micromass, model 602 (twin collector)

3.2.2.2 Application of ^{15}N in the Field

The presence of ^{15}N in a volume of soil at a given location will be referred to as an inplant in the following descriptions.

In 1984 and 1985, three 34-m rows of thistles 2 m apart, with plants 15 cm apart, were planted at the 5 to 6-leaf stage, with the peat pots in which they were first grown in the greenhouse. The part of each pot that was above the soil surface was then torn off, since it would have served as a moisture wick. The plants were well watered every 2 days for the first week after planting to permit good establishment. ^{15}N inplants were made at 15, 30, 45 or 60 cm depth every 2 m in each row. Inplants made at a given depth were contiguous in a row. Thus, in a 34-m long row, there were four inplants at 15 cm depth every 2 m and along a continuous 8 m. In 1984, each inplant consisted of 1 ml $^{15}NH_4Cl$ (38 mg/ml), containing 10 mg ^{15}N, and in 1985 of 1 ml $^{15}NH_4Cl$ (19 mg/ml), containing 5 mg ^{15}N.

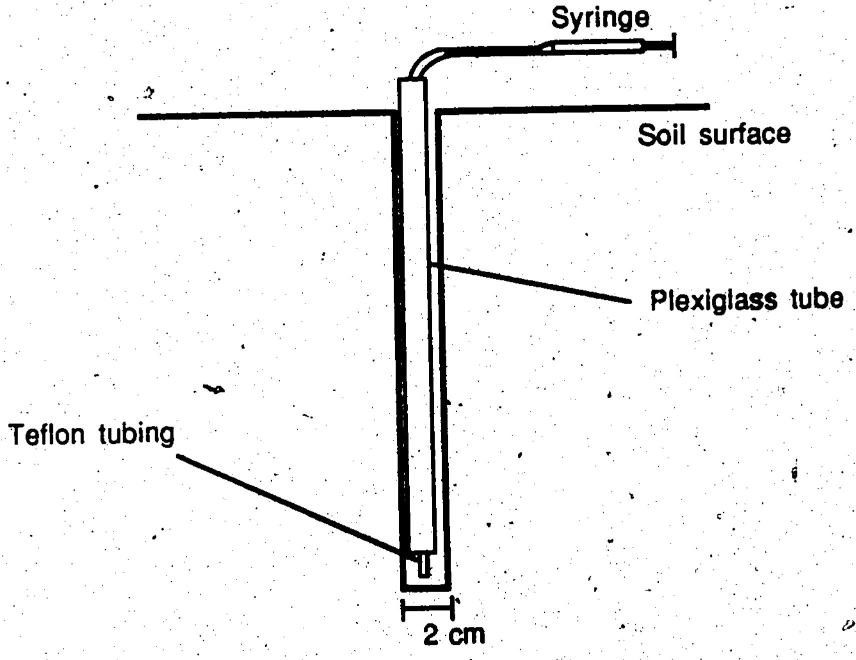

Figure 2. Method for adding ^{15}N below the soil surface.

A hole 2 cm in diam was drilled in the soil to the depth of the inplant and a plexiglass tube 0.5 cm diam and slightly shorter than the desired depth was inserted. A 1-ml microsyringe with 1-mm diam Teflon ^{TM} tubing attached to its needle was filled with the $^{15}NH_4Cl$ solution and inserted into the plexiglass tube. The tubing was slightly longer than the plexiglass tube and shorter than the depth of the inplant (Figure 2). After the microsyringe was emptied, the Teflon^{TM} tubing was removed from the plexiglass tube, followed by removal of the tube. This precaution was taken to prevent vertical spreading of $^{15}NH_4Cl$ along the hole.

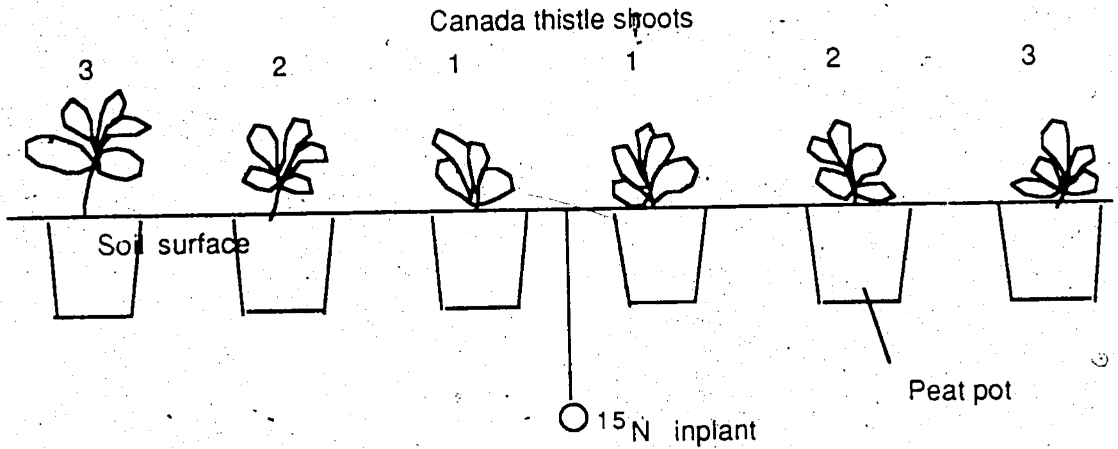

Figure 3. Numbering of thistle shoots in a row in which a ^{15}N inplant was made.

One week after planting, ^{15}N inplants were placed at the 15-cm and 30-cm depths, and one week later sampling started. The two plants on each side of the inplant and closest to it for the shallowest depth were sampled first (shoots 1, Figure 3). These plants were in pots 3.75 cm away from the site of the inplant. The second sampling consisted of the plants second closest to the 15-cm inplants (shoots 2, Figure 3), 18.75 cm away from the site of the inplant, and of the closest plants to the site of the 30-cm inplants. At that time, ^{15}N inplants were placed for the 45 and 60-cm depths. At the third sampling time, the plants third closest to the 15-cm inplants (shoots 3, Figure 3), 33.75 cm away, were sampled, as well as the plants second closest to the 30-cm inplants, and the closest thistles to the 45-cm inplants. Six samplings were done, with the sixth consisting of the plants third closest to the 60-cm inplant. In 1984, but not in 1985, a seventh sample was taken, consisting of the secondary shoots closest to the 15-cm inplants.

Sampling was done weekly in 1984, but in 1985, it was done every 4 days. Samples composed of two plants each were measured for height and their leaves were counted. They were then ground in a Wiley mill, digested following the Kjeldahl analysis, and the $^{15}N/^{14}N$ ratio was identified with a mass spectrometer as described earlier. Means and standard errors of the means of the percentage of the total nitrogen in the form of ^{15}N were calculated.

Knowing that the thistle shoots were 15 cm apart and that the pots were 7 cm deep and 7.5 cm wide, and assuming that the roots of each plant filled every pot, the rate of expansion of the root system was estimated. For example, shoots could contain ^{15}N 22 cm from the site of the 15-cm inplant 21 days after thistles were planted. In 21 days the roots grew 8 cm deep (depth of inplant less depth of pot) and 18.75 cm horizontally, or a diagonal distance of $(18.75^2+8^2)^{0.5} = 20$ cm.

3.3 Effects of Nitrogen on Canada Thistle

3.3.1 Nutrient Solution

Two rates of nitrogen were chosen, 21 and 210 ppm. The 21 ppm nitrogen concentration was similar to the nitrogen level in untreated topsoil at the Edmonton Research Station site (Appendix 3), while the 210 ppm nitrogen concentration was reported to be close to the upper limit of the nitrogen level to which Canada thistle root bud dormancy would respond (McIntyre and Hunter, 1975). The optimum level of nitrogen for releasing Canada thistle root bud dormancy varied between 70 and 210 ppm nitrogen, depending on the source of information (Hamdoun, 1970; McIntyre and Hunter, 1975). NH_4NO_3 was chosen as the source of nitrogen, since it was reported to be efficient in releasing root bud dormancy when using nutrient solution (McIntyre and Hunter, 1975).

The experiment was conducted in a growth room at a 25/15°C day/night temperature regime and a 16-hour photoperiod. The experiment was carried out in two trials, the first trial at a light intensity of 150 $\mu E.m^{-2}.sec^{-1}$, and the second trial at a light intensity of 250 $\mu E.m^{-2}.sec^{-1}$. Canada thistle plants were washed out of peat pots and transplanted into silica sand (4 to 12 mesh/cm) in 13-cm diam plastic pots. Nine pots were fitted in one tray which served as a replication of one treatment. Each treatment had two replications. Two different nutrient solutions were used as the two treatments. The nutrient solutions were modifications of Hoagland's solution (1950), as described in Table 1, and differed only in their nitrogen concentrations. Every two days, the sand of each pot was leached with water and the Canada thistle plants were fertilized immediately with 100 ml of the appropriate nutrient solution.

Plants were sampled at the 17 to 21-leaf stage, or 7 weeks after planting for the high nitrogen treatment, and 10 weeks after planting for the low nitrogen treatment. Roots were divided into small roots (0.5 mm < diam < 1.5 mm), medium roots (1.5 mm < diam < 2.5 mm) and large roots (diam > 2.5 mm). These categories were chosen to group the large roots with secondary thickening into one category and to obtain approximately the same biomass of roots in the medium and small root diameter categories. Number, height, dry weight, and nitrogen content of

Table 1. Chemical composition of nutrient solutions of two different nitrogen concentrations.

Molecular Concentration		Elemental Concentration	
Chemical	Concentration	Element	Concentration
	(μM)		(ppm)
		Macronutrients	
K_2PO_4	2000	K	239
KCl	2000	Ca	160
$CaCl_2$	4000	P	62
$MgSO_4.7H_2O$	1000	S	32
		Mg	24
		Micronutrients	
KCl	50	Cl	239
H_3BO_3	25	B	0.27
$MnSO_4.H_2O$	2	Mn	0.11
$ZnSO_4.H_2O$	2	Zn	0.13
$CuSO_4.5H_2O$	0.5	Cu	0.03
H_2MoO_4	0.5	Mo	0.05
Fe Edta	20	Fe	1.12
		Low Nitrogen Solution	
NH_4NO_3	750	N	21
		High Nitrogen Solution	
NH_4NO_3	7500	N	210

aboveground shoots, height and number of underground shoots, and root length of small, medium and large roots were recorded for each Canada thistle plant. On five plants of each replicate, the numbers of non-emerged and emerged root buds were determined for each root diameter category. Number of non-emerged and emerged root buds per meter of root were also calculated for each diameter category. Weighted averages for the entire plant were determined using the values of parameters measured for the entire plant, divided by the total root length of the plant. On the remaining four plants of each replicate, dry weight and nitrogen content for each root diameter category were determined. A Student t-test was used to compare means.

3.3.2 Soil

The nitrogen source used in experiments with soil as a growth medium was urea (46-0-0)[6]. Treated stands received the equivalent of 100 kg/ha nitrogen, with the exception of the experiment on the effect of nitrogen on shoot production done in 1984, where 70 kg/ha nitrogen was used. The nitrogen was broadcast manually and incorporated in the top 10 cm with a hoe. Supplementary soil nitrogen in ppm was calculated from the rate of nitrogen in kg/ha, soil bulk density, and the volume of soil in which the nitrogen was incorporated. Since soil bulk densities varied from one experiment to another, a given rate of nitrogen did not correspond to the same level of supplementary nitrogen calculated in ppm in all experiments.

3.3.2.1 Shoot Production

The experiments were done in the field, in two different ways. Young stands

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[6] Alberta Wheat Pool, Edmonton

received only one application of nitrogen in spring, and progress of the effect was recorded weekly throughout the growing season. In old stands, nitrogen was applied at different times during the growing season to different plots.

3.3.2.1.1 Newly Established Stands

Canada thistle plants still in their respective peat pots were planted on May 18, 1984 at the University of Alberta Edmonton Research Station. The part of each pot that was above the soil surface was removed. The total area chosen for planting was 12 m wide by 30 m long, and two blocks wide by four blocks long, separated from each other by a 2-m walkway. Each block was 4 m by 5 m in size. Three Canada thistle plants were planted in the middle of each of the two blocks along each of the shorter sides of the area, while two Canada thistle plants were planted in each of the remaining four blocks. The plants were well watered every 2 days for the first week, to permit good establishment. Four blocks, grouped together in a two by two matrix, were treated with 70 kg/ha of nitrogen, which corresponded to an extra 38 ppm nitrogen in the top 10 cm of soil, at the time of establishment on May 18 1984, and with 100 kg/ha of nitrogen, which corresponded to an extra 54 ppm nitrogen in the top 10 cm of soil, on May 18 1985, one week after Canada thistle emergence. The other four blocks were left untreated (15 to 21 ppm nitrogen was already present, see Appendix 3). Shoots produced by the eight stands were counted weekly during the growing season of 1984 from June 2 to September 22 and for the first 6 weeks of the growing season of 1985 from May 30 to July 8. The areas covered by each stand were calculated from the average diameters of each stand since each one was circular. Densities of Canada thistle plants for each stand were calculated from the numbers of shoots present in each stand and the areas covered by each stand. On July 8 in 1985, four infestations were excavated to examine the root system. On May 22 in 1986, about one week after Canada thistle emergence, 100 kg/ha of nitrogen was applied to the four remaining infestations. Shoot densities of each stand were calculated weekly from the number of shoots determined in four 0.5-m^2 quadrats placed randomly in each stand, from May 12 to June 30. Means and standard errors of the means were calculated for both the treated and untreated stands.

3.3.2.1.2 Stand Established for more than 10 Years

Sixteen 1 by 4 m blocks were staked out in an 11 and 12-year old stand, in 1985 and 1986, respectively, situated at the University of Alberta Ellerslie Research Station. Each block was divided into two parts. Canada thistle shoots of the entire block were cut to 15 cm above the soil surface before nitrogen application to half of each block. The treated halves received 100 kg/ha of nitrogen, which corresponded to an extra 61-ppm nitrogen in the top 10 cm of soil; the remaining halves were left untreated (10 to 35 ppm N was already present, see Appendix 3). The sixteen blocks were divided randomly into four sets of four blocks each.

In 1985, nitrogen was applied on the first set of blocks on June 9, 4 weeks after thistle emergence. Nitrogen was applied on the second set of blocks on August 3, 12 weeks after thistle emergence, on the third set on August 26, 14 weeks after emergence, and on the fourth set on September 29, 18 weeks after emergence. In 1986, the nitrogen applications were made on May 17, July 24, August 25 and on September 20, corresponding to 1, 11, 14 and 17 weeks after emergence, respectively.

Shoots produced on each half of the blocks were counted 4 weeks after the nitrogen was applied, with the exception of the shoots growing after the last nitrogen application in September, which were counted on May 17, 1986 and May

13, 1987. A paired Student t-test was done on the ratio of the number of shoots produced 4 weeks after the parent shoots were cut to the number of parent shoots for each time of nitrogen application.

3.3.2.2 Growth of the Root System

In the following experiments, nitrogen was applied once at the 5 to 6-leaf stage of the Canada thistle. Roots of container-grown Canada thistle were collected from the soil by sieving the soil with a 16-mesh screen to recover roots larger than 0.5 mm in diam in container-grown Canada thistle plants. This was not done for the one and two-year old Canada thistle stands, since only roots with a diameter larger than 1 mm were collected. Soil clods would easily break along these large roots.

3.3.2.2.1 Container-grown Canada Thistle Plants

Experiment 1, which lasted 7 weeks, was done outdoors at the Edmonton Research Station in 1986, from May 20 to July 16, and indoors under the growthroom conditions mentioned previously in section 4.2.1. The light intensity in the growthroom was 250 $\mu E.m^{-2}.sec^{-1}$. Experiment 2, which lasted 13 to 14 weeks, was done at the Edmonton Research Station during the growing seasons of 1985 and 1986 from June 2 to September 4-10, and from May 28 to August 29 - September 6, respectively.

In Experiment 1, eight 45 cm diam by 1-m deep containers, with eight 1-cm diam holes to permit drainage, were filled with Navarre clay loam. One Canada thistle plant at the 5 to 6-leaf stage, with its peat pot, was planted in each of the containers. The part of each pot above the soil surface was removed. The containers were divided into four replicates of two containers each. The soil of one of the containers of each replicate received 100 kg/ha of nitrogen, which corresponded to an extra 83 ppm of nitrogen in the top 10 cm of soil. The other containers received no additional nitrogen (10 to 12 ppm nitrogen was already present). The plants were watered every two days during the first week after planting in the outdoor trial. In the indoor trial, the plants received approximately 6 L water once at establishment, and then 1 L water each week, with the total amount corresponding to the amount received by the plants that were grown outdoors. Seven weeks after the initiation of the experiment, shoots and roots were harvested.

In Experiment 2, six large boxes were used. The boxes were 90 cm wide, 90 cm long and 1 m deep, with frames of welded angle iron, and sides of plywood. Two opposite sides functioned as sliding doors. The boxes were lined with plastic sheets to facilitate the removal of the doors at harvest time. One Canada thistle plant, with its peat pot, was planted in each of the boxes that had been filled previously with Navarre clay loam. The part of the pot above the soil surface was removed. The boxes were divided into three replicates, each consisting of two boxes. One box of each replicate received 100 kg/ha of nitrogen, which corresponded to an extra 83 ppm nitrogen in the top 10 cm of soil. The plants were then watered to field capacity every 2 days for the first week after planting. In the first trial, in 1985, because of the low precipitation, plants also received the equivalent of 1.85 cm of water on July 8. No further water was added to supplement the precipitation recorded in Appendix 6. Thirteen weeks after the initiation of the experiment, the thistle plants were harvested.

Number, dry weight, height and nitrogen content of shoots and of underground shoots were measured. The roots were then divided into small roots (0.5 mm < diam < 1.5 mm), medium roots (1.5 mm < diam < 2.5 mm) and large roots (diam > 2.5 mm).

In Experiment 1, each root category was divided into two equal parts on the basis of total fresh weight. One part of the root system was used for non-emerged and emerged root bud counts, while the other part was used for dry weight and nitrogen content determination. Root length was measured for both parts.

In Experiment 2, each root diameter category was divided into three parts on the basis of fresh weight. One part of each category was used to measure shoot production by planting root fragments, one part for root dry weight and nitrogen determination, and one part for non-emerged and emerged root bud counts. Root length was measured on parts used for the determination of shoot production by root fragments and for root bud determination.

The results obtained for all parameters were then adjusted for the entire root diameter category, by dividing the value obtained by the fresh weight of the part of the root system on which the measurement was taken, and multiplying the result by the total fresh weight of the root diameter category. Numbers of non-emerged and emerged root buds per meter of root as well as shoot production by root fragments per meter of root were calculated. Weighted averages were determined as in Section 4.3.1. A Student t-test was used to compare means.

3.3.2.2.2 One and 2-year old Canada Thistle Stands

The thistle stands excavated were the same as the ones studied for shoot growth in Section 4.2.2.1 and the excavation process was similar to the one described in Section 4.2.1. Canada thistle plants were cut on a 2 m wide by 4 m long area in each of the two treated and the two untreated stands in 1985 and 1986. These areas were then excavated to a depth of 2 m with a backhoe and the thistle roots were collected.

Six 10-cm thick slices were examined in each of the four trenches (Figure 1).

Root length was measured every 20 cm down the soil profile of each slice. Two slices in each trench were studied for root dry weight and, in 1986, also for nitrogen determination. Non-emerged and emerged root buds were counted for the roots collected in another two slices of each trench, and the remaining two slices were used to examine shoot production by root fragments. Roots from the first and last slices of each trench were always excavated as fast as possible and used for root bud determination since it had been reported that oxygen might affect root bud growth and initiation (McIntyre, 1979). For the remaining types of measurement one of the other four slices of each trench was chosen at random. Numbers of non-emerged and emerged root buds per meter of root, as well as shoot production by root fragments per meter of root were also determined.

3.4 Statistical Analysis

The data were not transformed. Standard errors of the means can lose their meaning if the interval scale properties of the data are not preserved. Student's t-test was used, since a departure from a normal distribution does not affect the outcome of a t-test, especially near the tails of the distribution (Steel and Torrie, 1980).

Because of the high variation inherent to Canada thistle plants and to root systems, the 0.1 level of probability was used to detect differences in effects of nitrogen treatments.

4. RESULTS AND DISCUSSION

4.1 Soil Properties and Environmental Data

Detailed soil properties and environmental data were recorded for 3 years at both the Ellerslie Reseach Station and the Edmonton Research Station sites. The values recorded are tabulated in Appendix 2 to 9, and are referred to only when necessary.

At the Ellerslie Research Station, recording of soil temperature at 10 cm depth began in May. No information was available for the Edmonton Research station for May. At both sites, soil temperatures from June 1 to September 1 in 1984, 1985, and 1986, had an average maximum of 18°C, which varied between 12°C and 20°C, and an average minimum of 13°C, which varied between 8°C and 18°C. In May 1986 at the Ellerslie Research Station, soil temperatures reached 26°C during three consecutive days. The soil remained unfrozen in October, the last month of recording. No information was available for the Edmonton Research Station for October.

4.2 Descriptive Study of the Root System

4.2.1 Root system of an Established Stand

Just prior to excavation, Canada thistle shoots were pruned to 15 cm above the soil surface at the early flowering stage. Mean stand density was 40 shoots /m^2 (dry weight 158 g/m^2).

The root system was sampled (Figure 4) to measure total root length, root dry weight, and number of root buds (Figures 5 to 7). In addition, the potential of these buds to develop into shoots was determined (Figure 8).

A few underground shoots were present in the top 40 cm of soil. An average of two was observed for each trench, i.e. for every three vertical soil slices excavated in each trench.

About one fourth of the total root mass was located in the top 20 cm of soil. The greatest part of the root system, therefore, occurred below this level (Figures 5 and 6). The highest root density for both the total root length and root dry weight was between 20 and 40 cm depth, and the density declined with increasing depth, below this level. The root system reached 1.8 m in depth.

Nearly half of the root buds were present in the top 20 cm of soil (Figure 7a). The number of root buds declined sharply with increasing depth. Very few buds occurred below 80 cm, and none was found below 120 cm.

The number of root buds per meter of root was also highest in the top 20 cm of soil (Figure 7b), and declined with increasing depth, generally by half the number present in the soil band immediately above the one observed.

No distinction was made in counting between emerged and non-emerged root buds, since it was observed that the time between sampling and treating the roots with lactic acid permitted some non-emerged root buds to emerge through the cortex.

Root buds on roots sampled in the top 40 cm of soil did not always produce shoots when the root pieces were planted in the greenhouse (Figures 7 and 8). In contrast, roots sampled deeper into the soil produced more shoots than the actual number of root buds present at sampling.

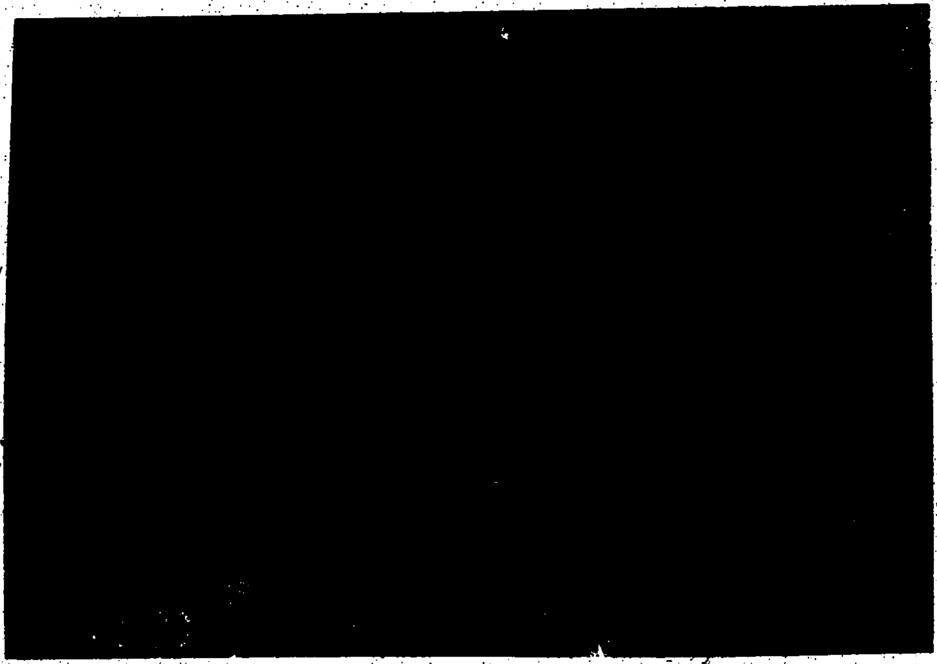

Figure 4. Trench in which roots of Canada thistle were sampled. The red flags divided the 20-cm soil bands.

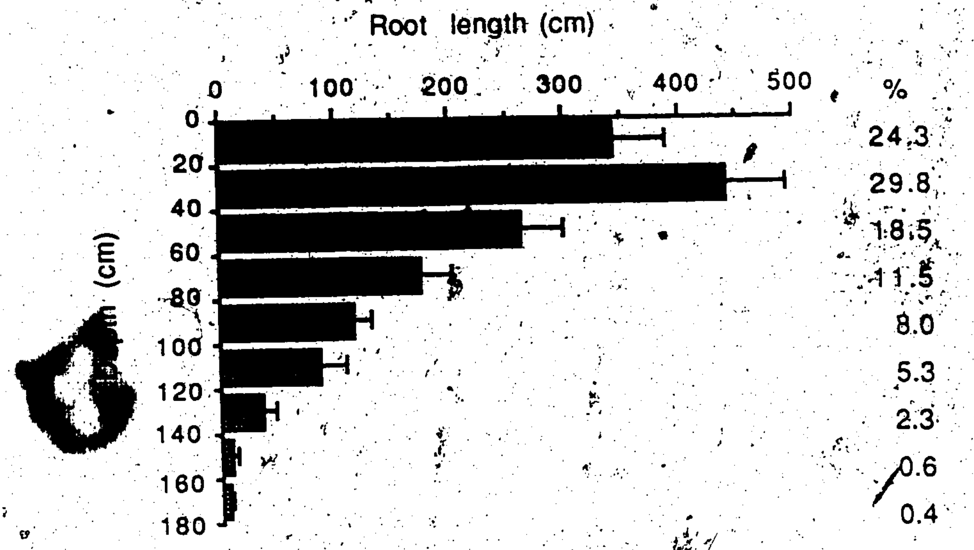

Figure 5. Average root length down the soil profile of a Canada thistle stand. The data represent the means for the roots found in twelve 2 m wide by 10 cm thick by 20 cm deep soil bands. Horizontal lines indicate standard errors of the means for each depth. The percentage distribution of the measurements down the soil profile is tabulated in the column.

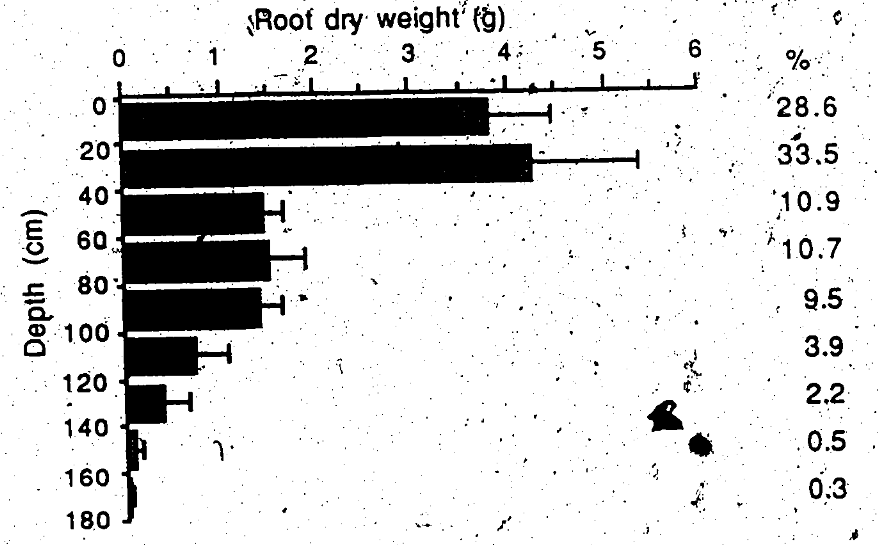

Figure 6. Average root dry weight down the soil profile of a Canada thistle stand. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 5 for more details.

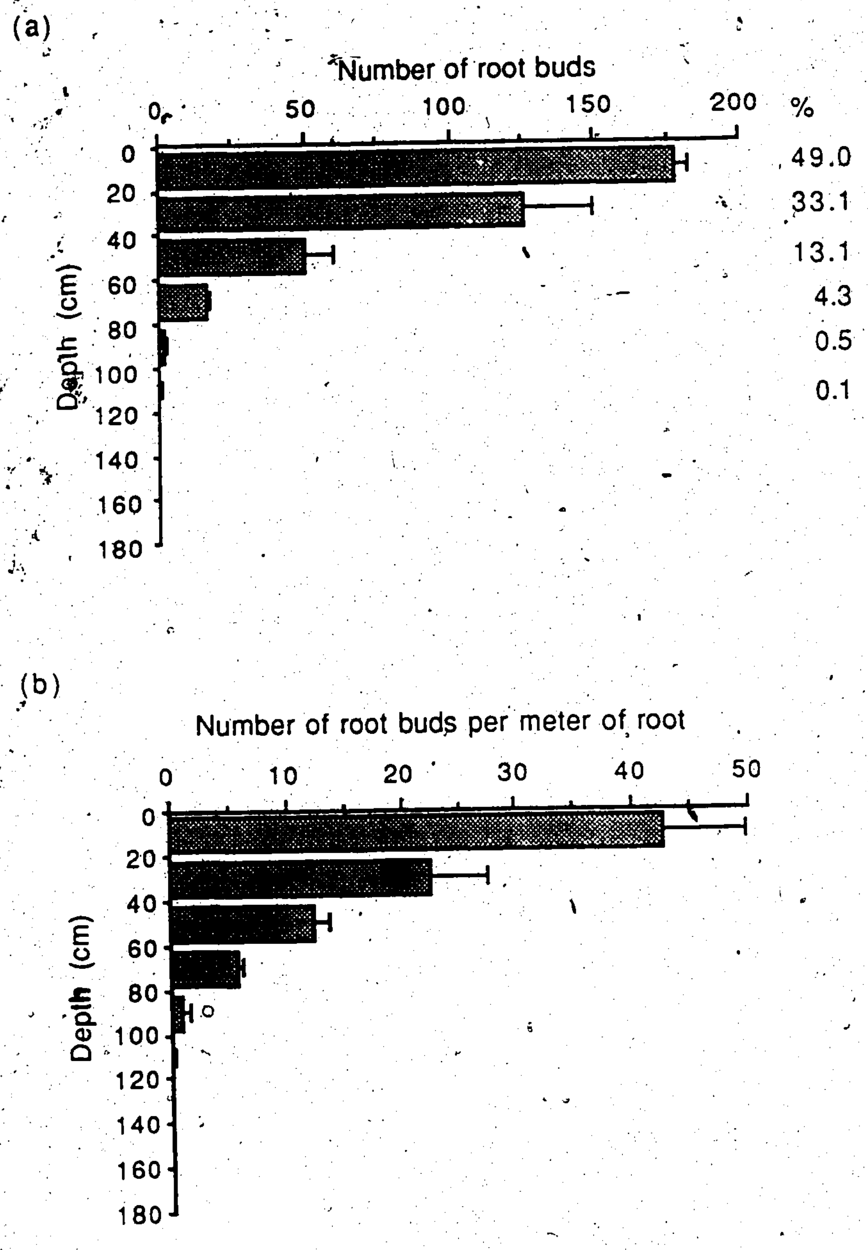

Figure 7. Average numbers of root buds (a) and root buds per meter of root (b) down the soil profile of a Canada thistle stand. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 5, page 43 for more details.

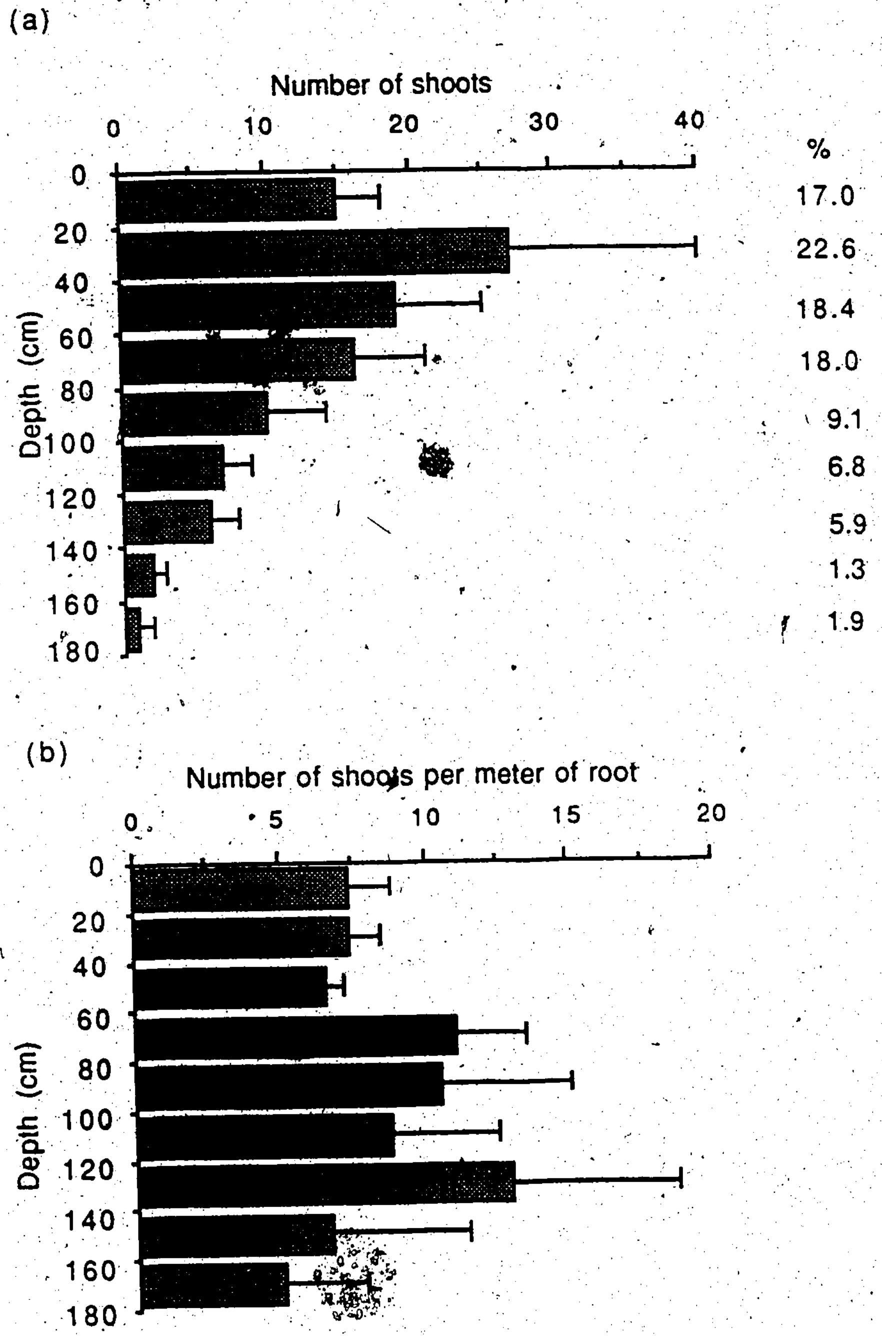

Figure 8. Average values for shoot production (a) and shoot production per meter of root (b) down the soil profile of a Canada thistle stand. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 5, page 43 for more details.

The number of shoots produced after replanting 10-cm-long root fragments sampled in each 20-cm wide soil bands, was similar for roots sampled between 0 and 100 cm depth (Figure 8a). The numbers declined with increasing depth below this level.

The shoot production per meter of replanted root was consistent for all root fragments and had a weighted mean of eight shoots per meter (Figure 8b). However, the number of root buds per meter of root decreased with increasing depth (Figure 7b). Thus, the depth at which a root was sampled affected the number of shoots produced per root bud present at sampling.

4.2.2 Rate of Root Expansion

^{15}N was detected throughout the plants 6 hours after 5 μg of ^{15}N was applied to the soil at a root tip (Table 2). Twelve hours after applying ^{15}N, the level of ^{15}N in leaves was slightly lower than 6 hours after ^{15}N application, but the level was relatively constant thereafter. Thus, it was concluded that ^{15}N was detectable in amounts larger than 0.40% in the leaves, the plant part sampled in the field, and that the levels did not change significantly over time.

The root system of any plant is composed of an intricate network of roots of various sizes, and straight pathways between two points in the root system would be expected. It was assumed, in calculating the rate of expansion of the root system in the field, that a relatively straight pathway existed between any point in the soil in contact with a root of a plant to the base of the shoot.

The ^{15}N levels detected in primary shoots (illustrated in Figure 9) collected in 1984 and 1985 were lower than the natural abundance. It was concluded, therefore, that Canada thistle roots did not reach the inplants, and that the actual

Table 2. Abundance of ^{15}N detected in treated plants 6 to 48 hours after application of ^{15}N to a root tip 10 cm away from the shoot.

Hours after Treatment	Shoot Height[a]	Leaf Number per Shoot[a]	Abundance of ^{15}N Three Youngest Leaves	Three Oldest Leaves	Untreated Roots	Treated Roots
	(cm)		(%X100)			
6	5±1	6±1	54.28	51.87	65.01	398.46
12	4±1	6±1	43.30	41.15	47.74	941.65
24	4±1	6±1	41.35	38.88	45.01	84.27
48	4±1	6±1	42.35	44.48	41.52	243.21

[a] Values ± standard error of the mean.

Figure 9. Row of Canada thistle 49 days after transplanting.

rates of expansion of the root systems were lower than the values calculated (Tables 3 and 4). The rate of expansion of the root system was estimated to be lower than 0.63 cm/day, the first calculated value, when primary shoots were young, under the growing conditions found in spring and early summer in Alberta.

When the production of leaves or secondary shoots increases, more carbohydrates should be produced and available for root growth. Thus, the rate of expansion of the root system would be expected to increase. To support this assumption, secondary shoots were sampled 7 weeks, or 49 days, after ^{15}N application in 1984 (Table 3). Elevated levels of ^{15}N were detected, and the rate of expansion of the root system was estimated as being equal to or higher than 0.95 cm/day.

Only a rough estimate of the rate of root expansion can be made. The average rate of expansion was lower than 1 cm/day between 5 and 13 weeks after planting a 10 cm long root piece of Canada thistle in a chernozemic soil, in spring and early summer in Alberta. Assuming that there are 105 days in a growing season in Alberta (Environment Canada, 1982) when root growth is possible, a newly established Canada thistle stand with its growth uninhibited by competition or chemical, cultural, or mechanical control methods would grow to at least a 1-m depth in a growing season and would expand horizontally by at least 2 m. Since these estimates were very conservative, it was decided that the depth of excavation of the root system of the 1-year old stand should be 2 m.

4.3 Effects of Nitrogen on Canada Thistle

In the next sections, roots from the three root diameter categories will be referred as large, medium and small (diam > 2.5 mm; 1.5 mm < diam < 2.5 mm; 0.5

Table 3. Abundance of ^{15}N found in Canada thistle shoots after treatment, and estimated rate of root growth, in 1984.

		1984				
		Leaf	Distance between Inplant and Shoot			Root Growth
Days[a]	Shoot Height[b]	Number per Shoot[b]	Vert.	Hor.	^{15}N[b]	Rate
	(cm)		(cm)	(cm)	(% X 100)	(cm/day)
14	5±1	7±1	8	4	36.67±0.02	<0.63
21	4±1	10±1	8	19	36.79±0.03	<0.97
			23	4	36.76±0.04	<1.11
28	8±1	14±1	8	34	36.76±0.04	<1.24
			23	19	37.10±0.22	<1.06
			38	4	36.99±0.11	<1.36
35	10±1	15±1	23	34	36.75±0.05	<1.17
			38	19	37.02±0.08	<1.21
			53	4	36.89±0.03	<1.52
42	16±1	15±1	38	34	36.87±0.09	<1.21
			53	19	36.89±0.04	<1.34
49	25±1	18±2	53	34	36.94±0.11	<1.28
56[c]	6±1	7±1	8	4	49.77±4.54	>0.16
			23	4	47.46±3.87	>0.42
			38	4	41.28±1.65	>0.68
			53	4	40.28±0.45	≥0.95

[a] Days after transplanting.

[b] Values ± standard error of the mean.

[c] Results obtained for secondary shoots.

Table 4. Abundance of ^{15}N found in Canada thistle shoots after treatment, and estimated rate of root growth, in 1985.

			1985			
Days^{a}	Shoot Height^{b}	Leaf Number per Shoot^{b}	Distance between Implant and Shoot Vert.	Hor.	^{15}N^{b}	Root Growth Rate
	(cm)		(cm)	(cm)	(% X 100)	(cm/day)
14	3±1	7±1	8	4	37.00±0.08	<0.63
18	3±1	7±1	8	19	36.90±0.03	<1.13
			23	4	36.89±0.06	<1.29
22	4±1	8±1	8	34	36.86±0.03	<1.58
			23	19	36.80±0.02	<1.35
			38	4	36.86±0.03	<1.74
26	4±1	9±1	23	34	36.82±0.02	<1.57
			38	19	36.86±0.02	<1.63
			53	4	37.99±1.08	<2.04
32	4±1	10±1	38	30	36.78±0.02	<1.59
			53	15	36.84±0.03	<1.76
38	5±1	12±1	53	30	36.79±0.02	<1.65

[a] Days after transplanting.

[b] Values ± standard error of the mean.

4.3.1 Nutrient Solution

In the first growth room trial, where light intensity was $150\,\mu E.m^{-2}.sec^{-1}$, the number of aboveground shoots was not significantly different for plants that had received the low and the high nitrogen treatments, but shoot height and dry weight were 56% and 57% higher, respectively, for the plants that were grown at the high nitrogen level ($P \leq 0.001$) (Table 5). The number of underground shoots per plant was twofold higher for plants growing under the high nitrogen level as under the low nitrogen level ($P = 0.09$) (Table 5).

Total root length and root dry weight were lower when plants were grown at the high nitrogen level compared to the low nitrogen level ($P \leq 0.001$) and, as a consequence, the shoot/root dry weight ratio was three times as high for plants grown at the high nitrogen level ($P = 0.001$) (Table 5).

Emerged and non-emerged root buds are illustrated in Figures 10 and 11, respectively. There was no difference in the number of emerged root buds per plant between treatments (Table 6). However, the weighted mean of emerged root buds per meter of root was higher ($P = 0.05$) for plants grown under the high than under the low nitrogen level (Table 6). Similarly, no difference in the number of non-emerged root buds per plant was observed (Table 6), but the weighted mean of non-emerged root buds per meter of roots was higher ($P = 0.1$) for plants grown under the high than under the low nitrogen level.

In this trial, evidence for the release of root bud dormancy by nitrogen was the production of more underground shoots and more emerged root buds per meter of root when the plants were grown under a high nitrogen level compared to a low nitrogen level. The results obtained agreed with the conclusion of Hamdoun (1970) and McIntyre and Hunter (1975), that a high nitrogen level did release root bud dormancy.

Table 5. Response of shoots and roots of Canada thistle plants grown from the 6-leaf stage to the 17-leaf stage in nutrient solutions of different nitrogen levels.

First Trial, 150 $\mu E.m^{-2}.sec^{-1}$

	Nitrogen Levels		
	21 ppm	210 ppm	P^a
	Aboveground Shoots		
Number	1	2	0.15
Height (cm)	16	25	0.001
Shoot Dry Weight (g)	1.56	2.45	0.001
	Underground Shoots		
Number	0.3	0.7	0.09
	Root Length (cm)		
Root Diameter (mm):			
>2.5	18	6	0.001
1.5 - 2.5	33	51	0.04
0.5 - 1.5	110	70	0.001
Total	272	167	0.001
	Root Dry Weight (g)		
Root Diameter (mm):			
>2.5	0.63	0.13	0.01
1.5 - 2.5	0.25	0.17	0.17
0.5 - 1.5	0.32	0.21	0.09
Total	1.83	0.87	0.001
Shoot/Root Dry Weight Ratio	0.96	2.92	0.001

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[a] Level of significance based on a two-tailed t-test.

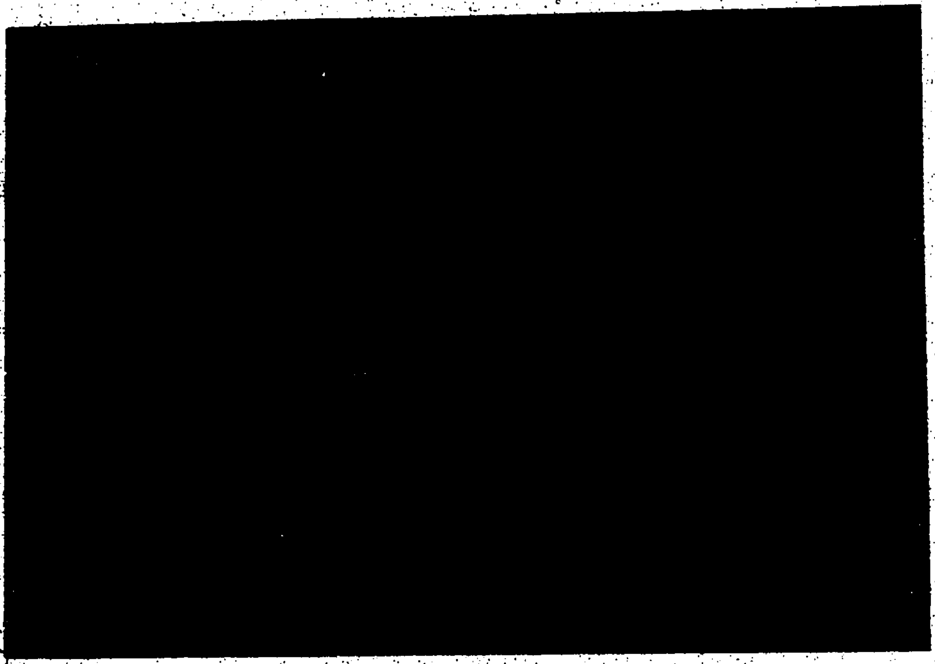

Figure 10. Emerged root buds (X5 magnificcation)

Figure 11. Non-emerged root buds (X5 magnification)

Table 6. Response of root buds of Canada thistle plants grown from the 6-leaf stage to the 17-leaf stage in nutrient solutions of different nitrogen levels.

First Trial, 150 $\mu E.m^{-2}.sec^{-1}$

Root Diameter (mm)	Nitrogen Levels 21 ppm	210 ppm	P[a]
	Emerged Root Buds per Plant		
>2.5	2	2	0.59
1.5 - 2.5	2	2	1.00
0.5 - 1.5	0	1	0.33
Total	3	3	0.69
	Emerged Root Buds per Meter of Root		
>2.5	26	24	0.95
1.5 - 2.5	6	7	0.89
0.5 - 1.5	0	1	0.33
Weighted Mean	1	2	0.05
	Non-emerged Root Buds per Plant		
>2.5	1	0	0.12
1.5 - 2.5	1	1	0.27
0.5 - 1.5	0	1	0.23
Total	1	2	0.46
	Non-emerged Root Buds per Meter of Root		
>2.5	3	6	0.14
1.5 - 2.5	2	6	0.20
0.5 - 1.5	0	4	0.19
Weighted Mean	1	2	0.10

[a] Level of significance based on a two-tailed t-test.

Two light intensities were used in the growth room experiment. Canada thistle plants seemed slightly etiolated after the first trial so the intensity was increased in the second trial.

In the second growth room trial, where light intensity was [illegible] $\mu E.m^{-2}.sec^{-1}$, the number of aboveground shoots produced when th[illegible]ts were growing under a high nitrogen level was lower than when plants were growing under a low nitrogen level ($P \leq 0.001$), but total shoot height and dry weight were 1.5 and as much as doubled when plants were grown under the high nitrogen level ($P \leq 0.001$) (Table 7).

The total number of underground shoots produced per plant averaged two for plants growing under both nitrogen levels, and the number of underground shoots per meter of root was not different between plants grown under both levels (Table 7).

Total root length was lower when using a high level of nitrogen than when using a low level of nitrogen ($P \leq 0.001$), but no difference in root dry weight was observed (Table 7). The shoot/root dry weight ratio was nearly three times as high for the plants growing under the high nitrogen level as under the low nitrogen level ($P \leq 0.001$) (Table 7).

No differences in total emerged root buds per plant or emerged root buds per meter of root were observed between treatments (Table 8). More emerged root buds per meter of large roots were produced by plants grown under the high nitrogen level than under the low nitrogen level ($P = 0.06$) (Table 8).

Total numbers of non-emerged root buds per plant and per meter of root were lower ($P \leq 0.001$ and $P = 0.09$, respectively) for the plants growing under the high nitrogen level than under the low nitrogen level. The high nitrogen level resulted in fewer non-emerged root buds on the large roots than did the low

Table 7. Response of Canada thistle shoots and roots grown from the 6-leaf stage to the 17-leaf stage in nutrient solutions of different nitrogen levels.

Second Trial, 250 µE.m^{-2}.sec^{-1}

	Nitrogen Levels		
	21 ppm	210 ppm	P^{a}
	Aboveground Shoots		
Number	5	3	0.001
Height (cm)	5	14	0.001
Dry weight (g)	2.26	5.27	0.001
	Underground Shoots		
Number	2	2	0.78
Height (cm)	3	2	0.04
Dry Weight (g)	0.40	0.17	0.001
Number per Meter	0.30	0.57	0.14
	Root Length (cm)		
Root Diameter (mm):			
>2.5	48	18	0.001
1.5 - 2.5	58	80	0.18
0.5 - 1.5	590	380	0.001
Total	691	476	0.001
	Root Dry Weight (g)		
Root Diameter (mm):			
>2.5	0.43	0.55	0.39
1.5 - 2.5	0.38	0.26	0.15
0.5 - 1.5	0.56	0.50	0.47
Total	2.62	2.27	0.15
Shoot/Root Dry Weight Ratio	0.86	2.43	0.001

[a] Level of significance based on two-tailed t-test.

Table 8. Response of root buds of Canada thistle plants grown from the 6-leaf stage to the 17-leaf stage in nutrient solutions of different nitrogen levels.

Second Trial, 250 $\mu E.m^{-2}.sec^{-1}$

Root Diameter (mm)	Nitrogen Levels 21 ppm	210 ppm	P^a
	Emerged Root Buds per Plant		
> 2.5	6	4	0.13
1.5 - 2.5	2	1	0.41
0.5 - 1.5	1	1	0.82
Total	8	5	0.22
	Emerged Root Buds per Meter of Root		
> 2.5	12	29	0.06
1.5 - 2.5	5	4	0.66
0.5 - 1.5	1	1	0.53
Weighted Mean	1	1	0.96
	Non-emerged Root Buds per Plant		
> 2.5	3	1	0.001
1.5 - 2.5	3	2	0.17
0.5 - 1.5	4	2	0.22
Total	11	5	0.001
	Non-emerged Root Buds per Meter of Root		
> 2.5	8	4	0.18
1.5 - 2.5	[illegible]	4	0.61
0.5 - 1.5	1	1	0.87
Weighted Mean	2	1	0.09

---

[a] Level of significance based on a two-tailed t-test.

nitrogen level (Table 8).

Nitrogen content of different plant parts was determined in both trials (Table 9). Nitrogen contents of the different parts of plants grown under the same nitrogen level were similar for both trials. The nitrogen percentage was 3 to 5 times higher in the high nitrogen treatment than in the low nitrogen treatment for both trials (Table 9).

The data in the second trial, where light intensity was higher than in the first trial, did not unequivocally support the release of root bud dormancy by nitrogen. Although the number of emerged root buds per meter of large root was higher when the plants were grown under the high nitrogen level than under the low nitrogen level, there was also some evidence against the release of root bud dormancy by nitrogen. The number of aboveground shoots was lower when the plants were grown under the high nitrogen level compared to the low nitrogen level ($P \leq 0.001$).

No definite explanation can be given, except that there might be some strong interaction between nitrogen levels, light intensity and root carbohydrate levels. From the results obtained in these two trials, no conclusions can be drawn about the effects of nitrogen on root bud dormancy.

4.3.2 Soil

Canada thistle stands were treated with 70 kg/ha nitrogen in one experiment, and with 100 kg/ha in all other experiments, which corresponded to a range of nitrogen concentrations of 59 to 119 ppm in the top 10 cm of soil (Appendix 3).

Table 9. Nitrogen content of dried shoots and roots of Canada thistle plants grown from the 6-leaf stage to the 17-leaf stage in nutrient solutions of different nitrogen levels.

	Nitrogen Content		
	Nitrogen Levels		
	21 ppm	210 ppm	P[a]
	(%)	(%)	
First Trial 150 µE. $m^{-2}.sec^{-1}$			
Aboveground Shoots	0.9	2.9	0.001
Root Diameter (mm):			
> 2.5	0.5	1.5	0.001
1.5 - 2.5	0.3	1.3	0.001
0.5 - 1.5	0.3	1.5	0.001
Second Trial 250 µE. $m^{-2}.sec^{-1}$			
Aboveground Shoots	1.1	3.3	0.001
Underground Shoots	0.8	2.9	0.001
Root Diameter (mm):			
> 2.5	0.4	2.2	0.001
1.5 - 2.5	0.4	2.2	0.001
0.5 - 1.5	0.5	2.1	0.001

---

[a] Level of significance based on a two-tailed t-test.

4.3.2.1 Shoot Production

Canada thistle stands were treated with nitrogen at the time of establishment on May 18 1984, and on May 18 1985, one week after Canada thistle emergence. The other four stands were left untreated. After excavating four stands in 1985, about one week after Canada thistle emergence in 1986, nitrogen was applied to two of the four remaining stands.

Linear, polynomial, logarithmic and exponential regressions were calculated for the data on shoot production, shoot density, and area covered by the young Canada thistle stands over time. Linear regressions were calculated for the transformed sigmoid portion of the data on shoot production and area covered by Canada thistle in 1984 (Figure 12). The best fitted regressions were represented by cubic equations. They lacked obvious biological meaning, and did not help in the interpretation of the data. Thus, the curves presented here are curves that pass through all the means.

It took 4 weeks, from May 18 to June 16, for secondary shoots to start appearing (Figure 12). By July 7, 7 weeks after planting, the plots that received 70 kg/ha nitrogen had produced twice as many shoots as the plots that received no nitrogen. From August 11 to August 30, 12 to 14 weeks after planting, the rate of shoot production increased. This increase was associated with the decreasing photoperiod occurring at that time in Alberta and with 20 mm precipitation recorded between August 13 and 27, and followed a period of high air temperature, the maximum air temperature averaging 32°C for the previous 3 weeks (Appendix 8). The shorter photoperiod would have increased the initiation of root buds (McAllister and Haderlie, 1985b). It is possible that the 32°C temperature promoted the growth of an increasing number of root buds, which surfaced after the

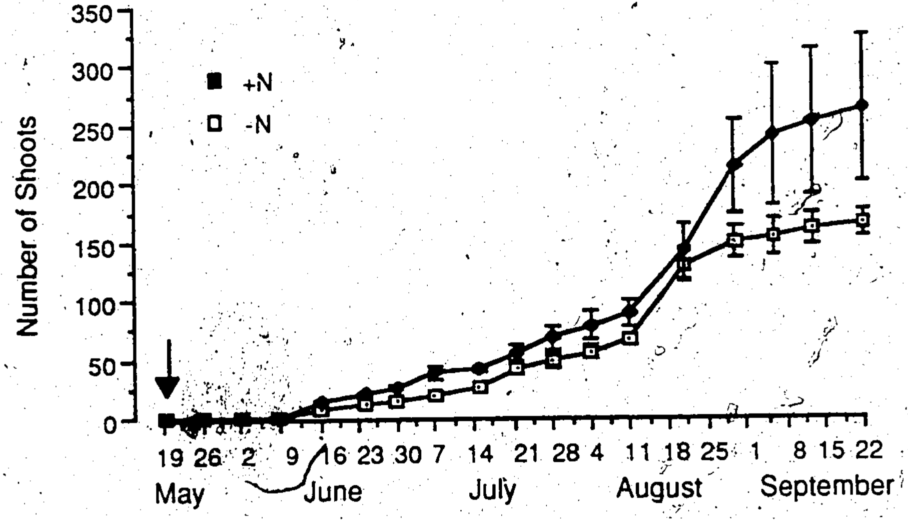

Figure 12. Shoot number of nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1984. Canada thistle was planted and treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

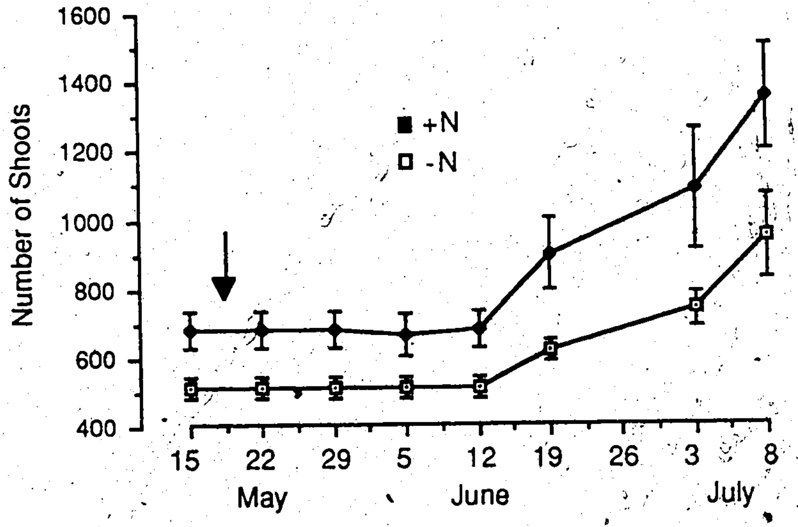

Figure 13. Shoot number of nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1985. Canada thistle was treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

beginning of the warm period (McAllister and Haderlie, 1985b). By the end of the summer, on September 22, plots that had received nitrogen had produced 250 shoots per plot, while plots on which no nitrogen was applied had produced 150 shoots per plot (Figure 12).

On May 30 in 1985, 2 weeks after application of 100 kg/ha nitrogen, 40% more shoots were counted on treated stands than on untreated stands, which corresponded to 700 and 500 shoots for treated and untreated plots, respectively (Figure 13). Root buds produced in 1984 probably were released from dormancy in May 1985, in conjunction with some root growth and root bud production that occurred between September 1984 and May 1985.

In 1985, as was observed in 1984, it took 4 weeks, from May 18 to June 12, before an increase in shoot production was observed for both treated and untreated plots (Figure 13). By July 8, when the shoots were in the early flowering stage, 44% more shoots had been produced on treated plots than on untreated plots. Average shoot numbers per plot were 1300 shoots for treated plots and 900 for untreated plots (Figure 13). Thus, one year, 1 month and 3 weeks after planting two or three plants in the middle of a plot area, an average of 1100 shoots was produced.

There was no difference in the area covered by each stand of Canada thistle in 1984 and 1985, except for 4 weeks at the end of 1984 (Figures 14 and 15). The increased rate of spread from July 28 to August 30 in 1984 was associated with a decreasing photoperiod, and increased air temperatures and precipitation from July 23 to August 13, as stated above (Appendix 8). Roots on the outside of stands were probably the ones that supported the least inhibited root buds. These root buds were far enough from the parent shoots to be able to compete successfully for water and nutrients, and the warm period promoted the growth of these buds

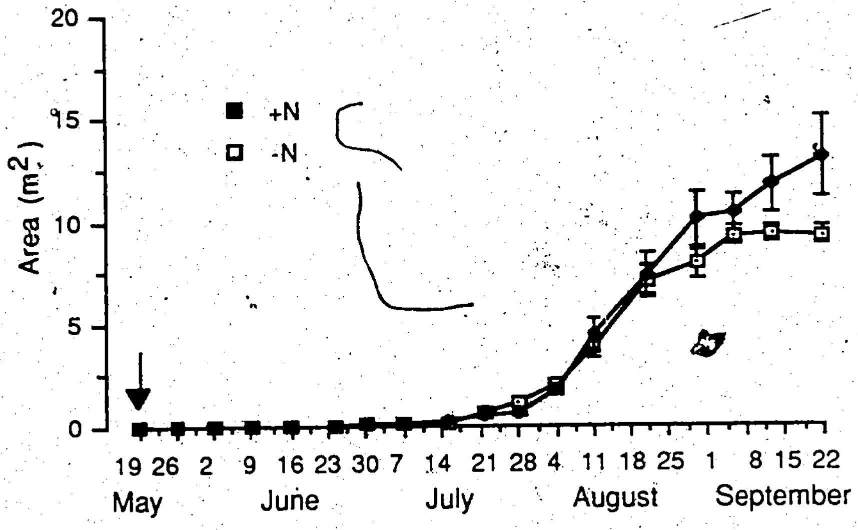

Figure 14. Area covered by nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1984. Canada thistle was planted and treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

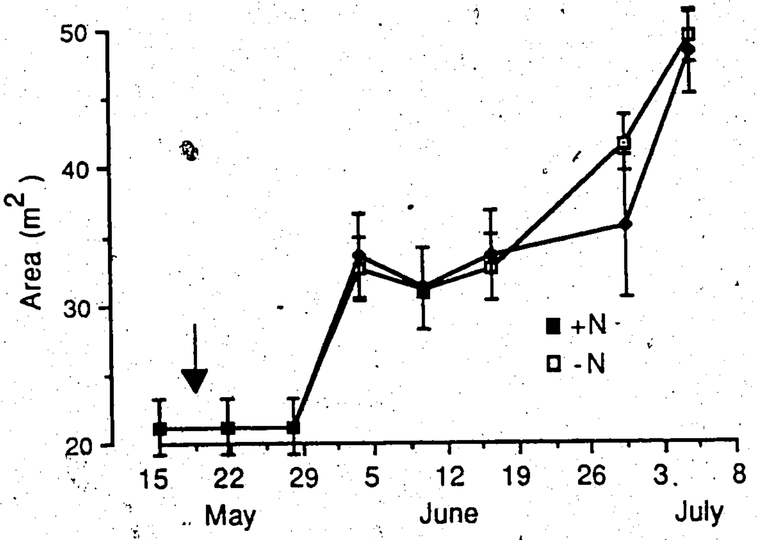

Figure 15. Area covered by nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1985. Canada thistle was treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

(McAllister and Haderlie, 1985b).

Shoot density of treated and untreated stands was as high as 400 and 200 shoots/m^2 in 1984, respectively (Figure 16). The increase in shoot density between June 2 and 24, or between 2 and 5 weeks after planting, implied that shoot production was continuing but that the area colonized by Canada thistle was not expanding. On June 24, shoots were at the early bud stage, the stage at which root carbohydrates and nitrogen are reported to be at their lowest (Arny, 1932; Welton et al., 1929). Thus, in theory, a given length of root at the early bud stage would have a lower shoot production than at any other time, and this could explain this reduction in shoot density.

No obvious relationship between the increase in shoot density and environmental data was observed. In 1984, nitrogen-treated stands produced a higher shoot density than untreated stands only between June 16 and July 15, or between 4 and 8 weeks after planting (Figure 16).

In 1985, from May 30 to July 8, from 2 to 7 weeks after emergence, the density of the stands that had received nitrogen was slightly higher than the stands that had received no nitrogen (Figure 17). A reduction in density for both treated and untreated stands was first observed when secondary shoots were colonising areas away from the parent shoots, starting on May 29 (Figure 15). On June 12, 4 weeks after nitrogen application, shoot density had stabilized to 24 shoots/m^2 in treated stands and 18 shoots/m^2 in untreated stands, and did not change for the rest of the growing season.

By May 28 in 1986, one week after nitrogen application, densities of shoots averaged 15 shoots/m^2 for treated stands and 14 shoots/m^2 for untreated stands. They remained at this level up to June 18, 4 weeks after nitrogen application, the

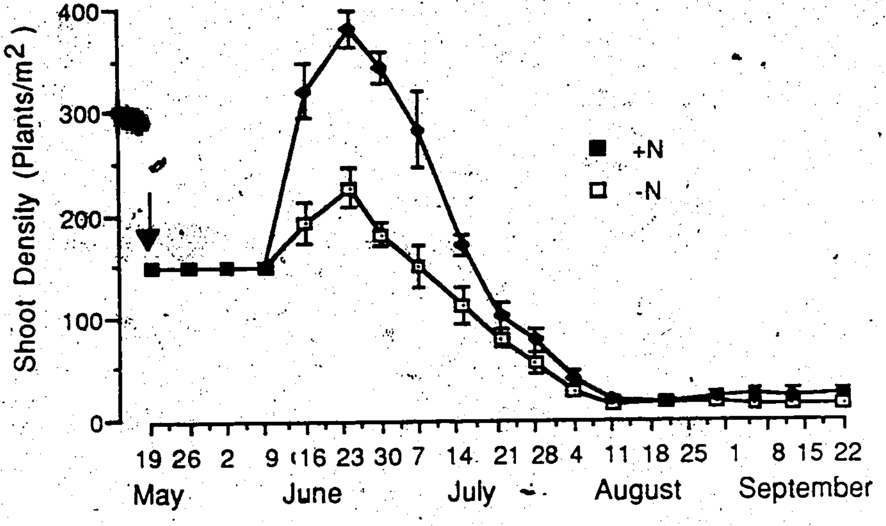

Figure 16. Shoot density of nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1984. Canada thistle was planted and treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

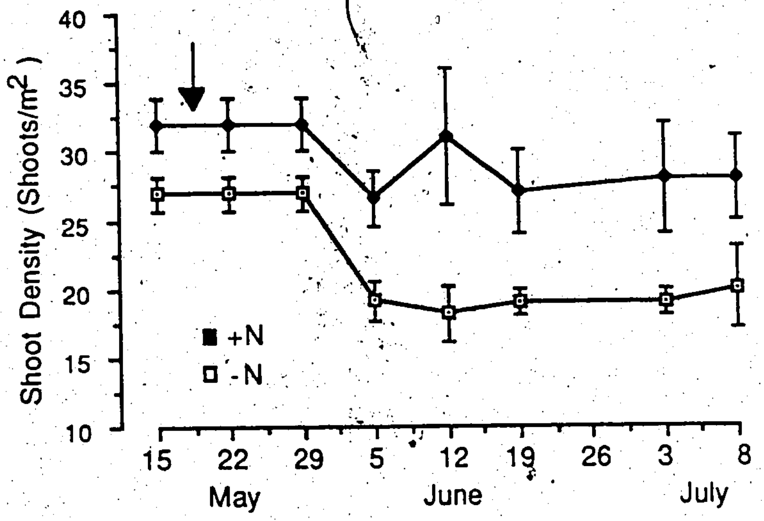

Figure 17. Shoot density of nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1985. Canada thistle was treated with nitrogen at the 5 to 6-leaf stage on May 18 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

last day of recording (Figure 18). The small difference between densities of treated and untreated stands probably was related to the saturation of the land's carrying capacity.

The densities of shoots decreased from 21 shoots/m^2 to 15 shoots/m^2 in 1985 and 1986. Although nutrient levels were not monitored over time, they possibly were getting low in the area that had been colonized from 1984 to 1986 and thus were restricting vigorous shoot growth in 1986. One could also infer that allelopathic chemicals had been produced (Bendall, 1975).

In an 11 and 12-year old stand, blocks of Canada thistle shoots were staked out, shoots were pruned, and half of each block received a nitrogen application (Table 10). The P values refer to a paired t-test, done on the ratios of shoot densities 4 weeks after treatment over the shoot densities at the time of treatment.

Nitrogen applied to plots on the second and fourth cutting dates resulted in 25% more shoots on treated plots than on untreated plots ($P = 0.09$; $P = 0.01$, respectively). Nitrogen applied on August 26 in 1985 resulted in a lower density than no nitrogen treatment ($P = 0.1$). This effe[illegible]rogen might be associated with a decreasing photoperiod and with high [illegible] humidity. The relative humidity during the 4 weeks following the [illegible]pplication on August 26 was higher than at any other recorded time in 1985 and 1986 (Appendix 8). However, it would be difficult to speculate why a decreasing photoperiod, coupled with high air relative humidity and with nitrogen treatments, would result in a reduction in shoot density compared to no nitrogen treatment. In 1986, only the nitrogen application at the second cutting date resulted in a higher shoot density compared to no nitrogen application ($P = 0.08$). This corresponded to 66% more shoots being produced in treated plots than in untreated plots (Table 10).

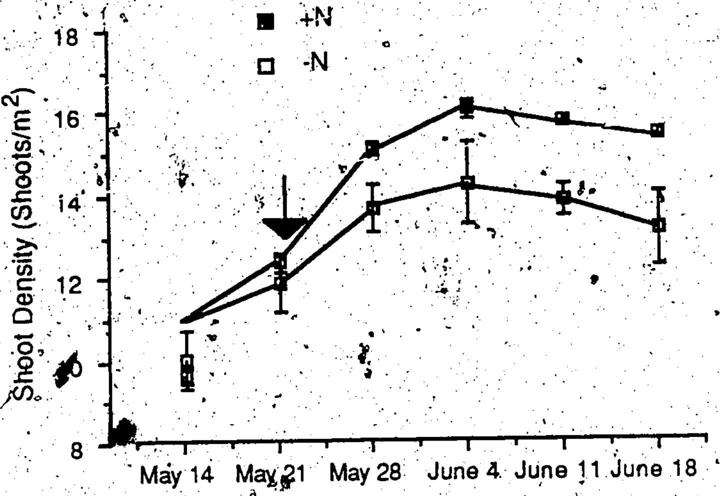

Figure 18. Shoot density of nitrogen-treated stands (+N) and untreated stands (-N) of Canada thistle in 1986. Canada thistle was treated with nitrogen at the 5 to 6-leaf stage on May 22 (see arrow). Vertical bars indicate standard errors of the means for each time interval.

Table 10. Canada thistle shoot production in response to two soil nitrogen levels after cutting the parent shoots in an 11 and 12-year old stand.

Date of Nitrogen Application	Weeks after Emergence	Shoot Density at Cutting		Shoot Density 4 Weeks after Cutting		
		-N	+N[a]	-N	+N	P[b]
1985						
June 9	4	6	6	25	30	0.18
Aug 3	12	24	25	40	50	0.09
Aug 26	14	29	30	2	1	0.10
Sept 29	18	25	26	50	63[c]	0.01
1986						
May 17	1	28	28	40	45	0.50
July 24	11	19	21	36	60	0.08
Aug 25	14	25	23	6	7	0.86
Sept 20	17	31	29	27	51[d]	0.15

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[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha of nitrogen was applied.

[b] Level of significance based on a paired two-tailed t-test, done on the ratios of shoot densities 4 weeks after cutting over the densities at cutting.

[c] Shoots counted on May 17, 1986.

[d] Shoots counted on May 13, 1987.

On August 25 and 26, in 1985 and 1986, respectively, low shoot densities were observed. This could be associated with a decreasing photoperiod (McAllister and Haderlie, 1985b).

The high nitrogen treatment resulted, in most cases, in a higher shoot density compared to the low nitrogen treatment. However, the origin of this increase is not obvious. The results obtained from the plants grown under two nitrogen levels in nutrient solution were not conclusive, and cannot be used for extrapolation. The higher shoot density obtained in treated plots might be the result of a higher shoot production per meter of root than in untreated plots, i.e. the result of releasing root bud dormancy. On the other hand, it could be the result of a higher root production in treated plots than in untreated plots, with no difference in the number of shoots per meter of root. To examine this in more detail, root systems of Canada thistle grown in soil were excavated after various time of exposure to nitrogen.

4.3.2.2 Growth of the Root System

4.3.2.2.1 Container-Grown Canada Thistle Plants

In Experiment 1, plants were exposed to two nitrogen levels between the 5th and 13th week after a root fragment had been planted. Sampling occurred at the early flowering stage of the plant. In Experiment 2, plants were exposed to two nitrogen levels between the 5th and 17th week after planting. Experiment 1 was done in two trials, one outdoors and one indoors. Experiment 2 was also done in two trials, both of them outdoors, one in 1985 and the other in 1986.

In the outdoor trial of Experiment 1, no differences in aboveground and underground shoot characteristics, root dry weight, and shoot/root dry weight ratios were observed (Table 11). Root length of treated plants, although about half the value of the untreated plants, was not statistically different from it, due to high standard error (P = 0.18) (Table 11).

No difference in the total number of emerged root buds per plant or per meter of root was observed, but the number of emerged root buds per meter in large roots was five times higher in treated plants than in untreated plants, with 35 and 7 root buds being produced per meter root in treated and untreated plants, respectively (P = 0.05) (Table 12).

There was no difference in the number of non-emerged root buds per plant. However, there were more non-emerged root buds produced per meter of large and medium root in treated plants than in untreated plants (P = 0.09; P = 0.08, respectively).

In the indoor trial of Experiment 1, aboveground shoots were not affected by nitrogen, nor were [illegible] shoots (Table 13). No differences in total root length or root dry weight were observed (Table 13), nor any differences in the number of emerged or non-emerged root buds per plant or per meter of root (Table 14). Nitrogen levels in the different plant parts were very similar for both treated and untreated plants, and for both outdoor and indoor trials (Table 15), with the exception of the nitrogen content of large roots of plants in the indoor trial, which was higher in nitrogen treated plants than in untreated plants (P = 0.09). No obvious relationship between nitrogen content of plants and effects of nitrogen levels of the growth medium on Canada thistle plants was observed.

The difference in results between the two trials of Experiment 1 was associated with environmental conditions. The temperatures prevailing in the outdoor trial (Appendix 8) could have resulted in a lower evapotranspiration than in the indoor trial, and thus in wetter conditions in the outdoor trial than in the

Table 11. Response of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 13th week after planting in 1986.

	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P[a]
	Aboveground Shoots		
Number	9	7	0.41
Height (cm)	15	15	0.92
Dry Weight (g)	29	20	0.37
	Underground Shoots		
Number	34	24	0.44
Height (cm)	9	9	0.80
Dry Weight (g)	2.24	1.61	0.37
Number per Meter	1.5	1.9	0.47
	Root Length (cm)		
Root Diameter (mm):			
> 2.5	131	62	0.34
1.5 - 2.5	414	414	0.99
0.5 - 1.5	1770	761	0.14
Total	2314	1238	0.18
	Root Dry Weight (g)		
Root Diameter (mm):			
> 2.5	2.21	0.90	0.39
1.5 - 2.5	1.49	1.94	0.60
0.5 - 1.5	0.88	0.55	0.33
Total	4.58	3.39	0.39
Shoot/Root Dry Weight Ratio	6.53	5.26	0.37

[a] Level of significance based on two-tailed t-test.

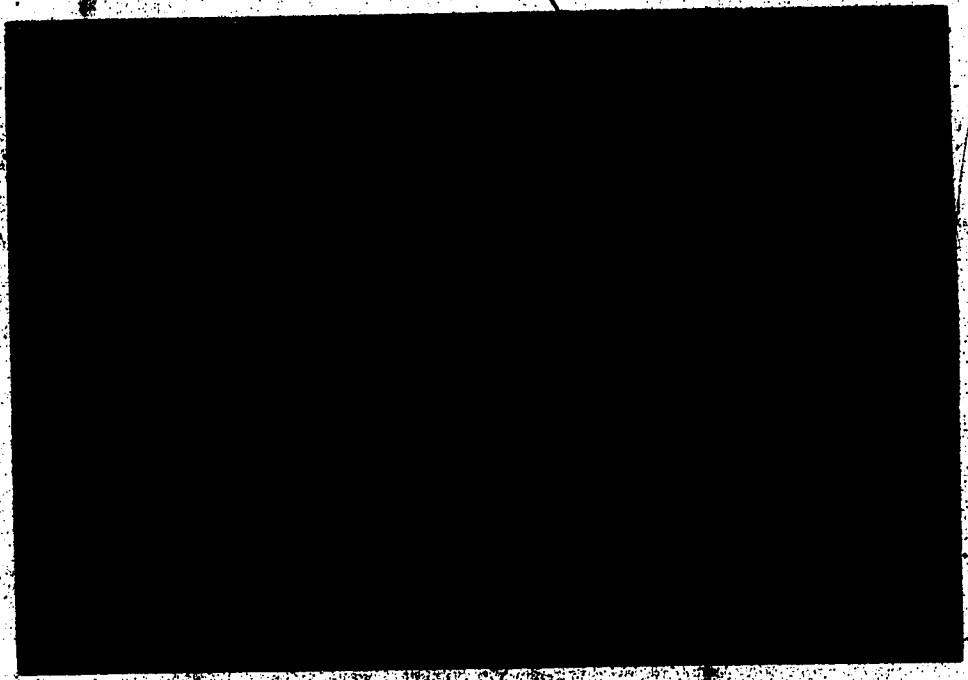

Figure 19. Canada thistle plants at harvest in Experiment 1.

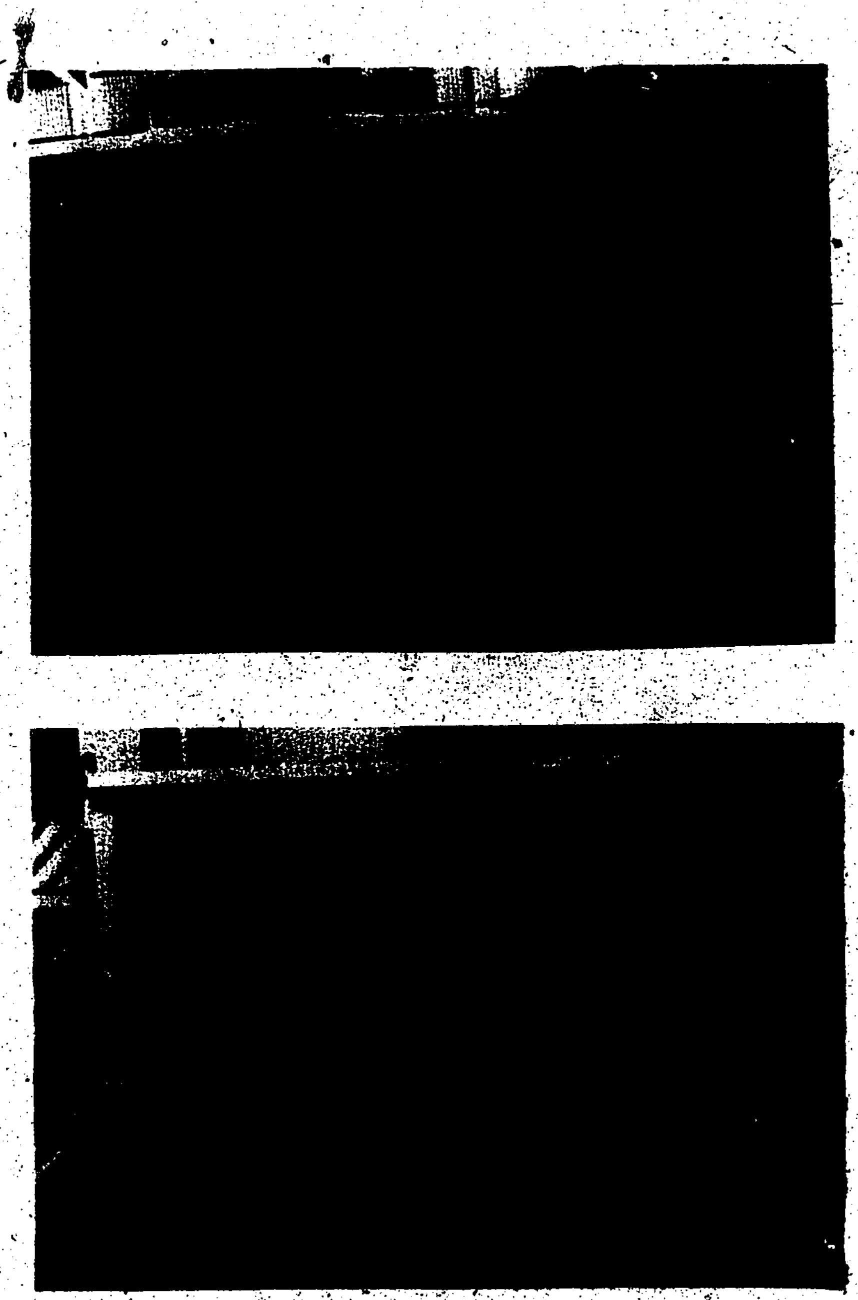

Figure 20. Canada thistle plant at harvest in Experiment 2.

Table 12. Response of root buds of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 13th week after planting in 1986.

	Nitrogen Applied		
Root Diameter (mm)	0 kg/ha	100 kg/ha	P[a]
	Emerged Root Buds per Plant		
>2.5	8	19	0.35
1.5 - 2.5	27	40	0.52
0.5 - 1.5	19	24	0.77
Total	54	83	0.49
	Emerged Root buds per Meter of Root		
>2.5	7	35	0.05
1.5 - 2.5	7	10	0.18
0.5 - 1.5	2	3	0.71
Weighted Mean	3	6	0.18
	Non-emerged Root Buds per Plant		
>2.5	11	16	0.60
1.5 - 2.5	61	88	0.49
0.5 - 1.5	38	38	0.97
Total	109	142	0.60
	Non-emerged Root Buds per Meter of Root		
>2.5	14	34	0.09
1.5 - 2.5	13	22	0.08
0.5 - 1.5	4	5	0.76
Weighted Mean	6	12	0.22

[a] Level of significance based on a two-tailed t-test.

Table 13. Response of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 13th week after planting under controlled conditions.

	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P^a
	Aboveground Shoots		
Number	7	6	0.68
Height (cm)	26	28	0.79
Dry Weight (g)	23	28	0.31
	Underground Shoots		
Number	14	16	0.64
Height (cm)	6	[illegible]	0.13
Dry Weight (g)	0.68	2.[illegible]	0.15
Number per Meter	0.5	0.6	0.50
	Root Length (cm)		
Root Diameter (mm):			
>2.5	217	122	0.13
1.5 - 2.5	436	487	0.74
0.5 - 1.5	1760	1908	0.77
Total	2413	2516	0.84
	Root Dry Weight (g)		
Root Diameter (mm):			
>2.5	6.04	3.56	0.15
1.5 - 2.5	4.11	4.61	0.83
0.5 - 1.5	2.32	2.36	0.94
Total	12.43	10.45	0.46
Shoot/Root Dry Weight Ratio	1.80	2.94	0.14

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[a] Level of significance based on a two-tailed test.

Table 14. Response of root buds of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 13th week after planting under controlled conditions.

	Nitrogen Applied		
Root Diameter (mm)	0 kg/ha	100 kg/ha	P[a]
	Emerged Root Buds per Plant		
> 2.5	22	18	0.71
1.5 - 2.5	12	13	0.93
0.5 - 1.5	2	4	0.40
Total	31	39	0.50
	Emerged Root buds per Meter of Root		
> 2.5	11	20	0.38
1.5 - 2.5	2	3	0.65
0.5 - 1.5	1	1	0.78
Weighted Mean	1	2	0.39
	Non-emerged Root Buds per Plant		
> 2.5	22	13	0.46
1.5 - 2.5	20	36	0.24
0.5 - 1.5	12	9	0.68
Total	59	52	0.65
	Non-emerged Root Buds per Meter of Root		
> 2.5	10	10	0.93
1.5- 2.5	4	7	0.29
0.5 - 1.5	1	0	0.29
Weighted Mean	2	2	0.65

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[a] Level of significance based on a two-tailed t-test.

Table 15. Nitrogen content of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 13th week after planting.

	Nitrogen Content		
	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P^a
	(%)	(%)	
Outdoors, 1986			
Aboveground Shoots	2.6	2.9	0.37
Underground Shoots	3.6	4.4	0.22
Roots			
Root Diameter (mm):			
>2.5	1.8	2.1	0.53
1.5 - 2.5	2.0	1.6	0.30
0.5 - 1.5	2.6	2.7	0.87
Indoors			
Aboveground Shoots	3.7	3.6	0.93
Underground Shoots	3.6	4.0	0.56
Roots			
Root Diameter (mm):			
>2.5	1.0	1.1	0.09
1.5 - 2.5	1.0	1.2	0.14
0.5 - 1.5	1.9	1.7	0.51

[a] Level of significance based on a paired two-tailed t-test.

indoor trial (Appendix 6). It is possible that the cold and wet conditions of the outdoor trial resulted in reduced root growth. As a result, the shoot/root dry weight ratio was much higher in the outdoor trial (5.9) than in the indoor trial (2.4).

Many other plant characteristics differed between the indoor and the outdoor trials, and these differences could also be related to the differences in temperature regimes or soil moisture levels between the two trials. An average of 1.7 underground shoots were counted per meter of root in the outdoor trial, compared to an average of 0.6 in the indoor trial (Tables 11 and 13). Similarly, in the outdoor trial, four emerged root buds and nine non-emerged root buds were produced per meter of root, compared to one emerged root bud and two non-emerged root buds per meter of root produced in the indoor trial (Tables 12 and 14).

Data obtained in Experiment 2 were very similar for both treated and untreated plants, but differed between trials. In the first trial of Experiment 2, carried out in 1985, no differences in number, height, or dry weight of aboveground shoots were observed between treated and untreated plants, nor any differences in underground shoot number, root length, or root dry weight (Table 16).

No differences in emerged or non-emerged root buds per plant or per meter of root were observed (Table 17). However, shoot production per plant and per meter of root after planting 10-cm long root fragments of each plant, was higher for the large roots of treated plants than for those of untreated plants (P = 0.03) (Table 17). The number of shoots produced per meter of replanted root was similar to the added numbers of emerged and non-emerged root buds produced per meter of root. However, the total number of root buds produced on large roots did not correspond as well to the number of shoots produced by replanted root fragments as did the number of root buds produced on medium and small roots.

In the second trial of Experiment 2, carried out in 1986, no differences in

Table 16. Response of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 18th week after planting in 1985.

	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P^a
	Aboveground Shoots		
Number	24	26	0.84
Height (cm)	25	32	0.34
Dry Weight (g)	151	180	0.17
	Underground Shoots		
Number	143	177	0.31
Height (cm)	16	16	0.70
Dry Weight (g)	30.5	43.5	0.23
Number per Meter	1.1	1.5	0.24
	Root Length (cm)		
Root Diameter (mm):			
> 2.5	919	1159	0.54
1.5 - 2.5	5105	4819	0.62
0.5 - 1.5	8027	5929	0.22
Total	14051	11907	0.31
	Root Dry Weight (g)		
Root Diameter (mm):			
> 2.5	27.4	46.4	0.22
1.5 - 2.5	60.3	68.3	0.69
0.5 - 1.5	19.2	46.7	0.36
Total	106.9	134.9	0.41
Shoot/Root Dry Weight Ratio	1.5	1.4	0.91

[a] Level of significance based on a two-tailed t-test.

Table 17. Response of root buds of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 18th week after planting in 1985.

	Nitrogen Applied		
Root Diameter	0 kg/ha	100 kg/ha	P^a
(mm)			
	Emerged Root Buds per Plant		
> 2.5	59	124	0.18
1.5 - 2.5	219	240	0.73
0.5 - 1.5	98	64	0.51
Total	376	428	0.63
	Emerged Root buds per Meter of Root		
> 2.5	7	12	0.38
1.5 - 2.5	4	5	0.56
0.5 - 1.5	2	1	0.37
Weighted Mean	3	4	0.21
	Non-emerged Root Buds per Plant		
> 2.5	51	67	0.11
1.5 - 2.5	84	267	0.28
0.5 - 1.5	56	41	0.63
Total	191	365	0.35
	Non-emerged Root Buds per Meter of Root		
> 2.5	[illegible]	6	0.67
1.5 - 2.5	2	5	0.27
0.5 - 1.5	1	1	1.00
Weighted Mean	1	3	0.31
	Shoot Production per Plant		
> 2.5	88	145	0.03
1.5 2.5	420	516	0.16
0.5 1.5	235	175	0.34
Total	742	732	0.96
	Shoot Production per Meter of Root		
> 2.5	12	13	0.03
1.5 - 2.5	8	11	0.16
0.5 - 1.5	3	3	0.34
Weighted Mean	5	7	0.96

[a] Level of significance based on a two-tailed t-test.

aboveground shoot characteristics were observed (Table 18). The underground shoots were 25% less numerous on treated plants than on untreated plants (P = 0.1). No differences in total root length or root dry weight were observed between treated and untreated plants (Table 18). However, large roots were 34% shorter in treated plants than in untreated plants (P = 0.07).

The total number of emerged root buds per plant was not different between treated and untreated plants (Table 19), although there were 70% fewer emerged root buds per plant on the medium roots of treated plants than on untreated plants (P = 0.06). On the other hand, there were twice as many emerged root buds per meter of large root in treated plants than in untreated plants (P = 0.09). No differences in the number of non-emerged root buds per plant or per meter of root were observed between treated and untreated plants. As for shoot production by replanted root pieces, there was more difference in shoot production by pieces of large roots than by pieces of medium or small roots, with 45% fewer shoots produced on the large roots of treated plants than on untreated plants (P= 0.09) (Table 19).

The number of shoots produced per meter of replanted root after planting root fragments was similar to the added numbers of emerged and non-emerged root buds produced per meter of root, with the number of root buds produced on large roots not corresponding as well to the number of shoots produced per meter of root as the number of root buds produced on medium and small roots.

The nitrogen levels of the different plant parts were similar for treated and untreated plants, in 1985, except for the aboveground shoots which had a much higher nitrogen level in treated plants than in untreated plants (Table 20). In 1986, there was no difference between the nitrogen levels of most parts of treated and untreated plants (Table 20), with the exception of the nitrogen content of medium roots of treated plants which was higher than for untreated plants (P = 0.01). These

Table 18. Response of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 18th week after planting in 1986.

	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P[a]
	Aboveground Shoots		
Number	26	28	0.55
Height (cm)	38	34	0.17
Dry Weight (g)	279	265	0.40
	Underground Shoots		
Number	169	127	0.10
Height (cm)	11	13	0.56
Dry Weight (g)	22.7	25.0	0.82
Number per Meter	1.8	1.5	0.33
	Root Length (cm)		
Root Diameter (mm):			
>2.5	1744	1153	0.07
1.5 - 2.5	4728	4025	0.19
0.5 - 1.5	3177	3540	0.23
Total	9649	8719	0.24
	Root Dry Weight (g)		
Root Diameter (mm):			
>2.5	53.7	39.8	0.39
1.5 - 2.5	62.6	51.4	0.21
0.5 - 1.5	12.7	11.3	0.71
Total	129.0	102.5	0.29
Shoot/Root Dry Weight Ratio	2.2	2.8	0.29

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[a] level of significance based on a two-tailed t-test.

Table 19. Response of root buds of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 18th week after planting in 1986.

	Nitrogen Applied		
Root Diameter	0 kg/ha	100 kg/ha	P[a]
(mm)			
	Emerged Root Buds per Plant		
> 2.5	58	75	0.58
1.5 - 2.5	199	117	0.06
0.5 - 1.5	81	52	0.37
Total	338	245	0.12
	Emerged Root Buds per Meter of Root		
>2.5	3	6	0.09
1.5 - 2.5	4	3	0.22
0.5 - 1.5	3	2	0.29
Weighted Mean	4	3	0.25
	Non-emerged Root Buds per Plant		
> 2.5	183	157	0.71
1.5 - 2.5	531	331	0.14
0.5 - 1.5	130	133	0.95
Total	844	622	0.13
	Non-emerged Root Buds per Meter of Root		
> 2.5	10	13	0.44
1.5 - 2.5	11	8	0.34
0.5 - 1.5	4	4	0.82
Weighted Mean	9	7	0.39
	Shoot Production per Plant		
> 2.5	298	165	0.09
1.5 - 2.5	560	567	0.96
0.5 - 1.5	262	287	0.74
Total	1120	1019	0.51
	Shoot Production per Meter of Root		
> 2.5	17	14	0.29
1.5 - 2.5	12	14	0.55
0.5 - 1.5	8	8	0.97
Weighted Mean	12	12	0.94

---

[a] Level of significance based on a two-tailed t-test.

Table 20. Nitrogen content of shoots and roots of Canada thistle plants grown from root pieces exposed to two soil nitrogen levels from the 5th to the 18th week after planting in 1985 and 1986.

	Nitrogen Content		
	Nitrogen Applied		
	0 kg/ha	100 kg/ha	P^a
	(%)	(%)	
1985			
Aboveground Shoots	2.6	4.2	0.001
Underground Shoots	2.6	3.4	0.16
Roots			
Root Diameter (mm):			
> 2.5	0.8	1.0	0.26
1.5 - 2.5	0.8	1.1	0.28
0.5 - 1.5	0.9	1.0	0.21
1986			
Aboveground Shoots	3.4	3.6	0.58
Underground Shoots	3.3	3.4	0.70
Roots			
Root Diameter (mm):			
> 2.5	1.2	1.2	0.96
1.5 - 2.5	1.2	1.7	0.01
0.5 - 1.5	1.4	1.4	1.00

---

[a] Level of significance based on a two-tailed t-test.

observations, coupled with the observation that treated plants had 70% fewer emerged root buds per plant than untreated plants, cast some doubt upon the theory that nitrogen could release root bud dormancy.

The results obtained in the two trials of Experiment 2 are very different. In 1986, there were 160% more non-emerged root buds per plant than in 1985. This corresponded to an average of 278 non-emerged root bud per plant produced in 1985, compared to 733 in 1986, and an average of two non-emerged root buds per meter of root in 1985 compared to eight in 1986. Shoot production after planting root fragments was also much lower in 1985, with 737 and 1070 shoots being produced per plant in 1985 and 1986, respectively. Similarly, six shoots per meter of replanted root were produced from root pieces in 1985 compared to 12 shoots per meter in 1986. One major reason for obtaining such different results between trials could be the lower precipitation during the first trial (1985) than during the second trial (1986) (Appendix 8). The nitrogen content of roots or the growth stage of the plants at sampling did not differ between the two years, and thus cannot be related to root bud production.

The outdoor trial of Experiment 1, which was done in 1986, and the 1986 trial of Experiment 2 did not give similar results. In Experiment 1, 4 and 1.4 times as many emerged and non-emerged root buds per meter of large root were observed in treated plants, respectively, compared to untreated plants (Table 12), while in Experiment 2, half as many emerged root buds per meter of large roots were observed for treated plants compared to untreated plants (Table 19).

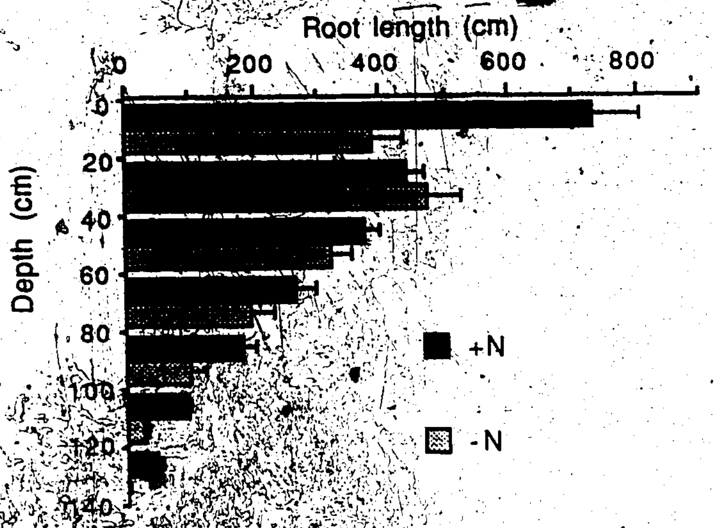
In Experiments 1 and 2 the entire root system was studied, without paying any attention to the distribution of the roots in the soil profile. The roots in the top 10 cm of soil, in which the nitrogen had been incorporated, might have been more drastically affected by nitrogen than the entire root system.

4.3.2.2.2 One and Two-year old Canada Thistle Stands

Just prior to excavation of the 1-year old stand, the nitrogen-treated plots had produced an average of 718 g/m^2 of shoot dry matter, and the untreated plots had produced an average of 611 g/m^2 of shoot dry matter. This production corresponded to 22 and 18 plants/m^2 for treated and untreated plots, respectively.

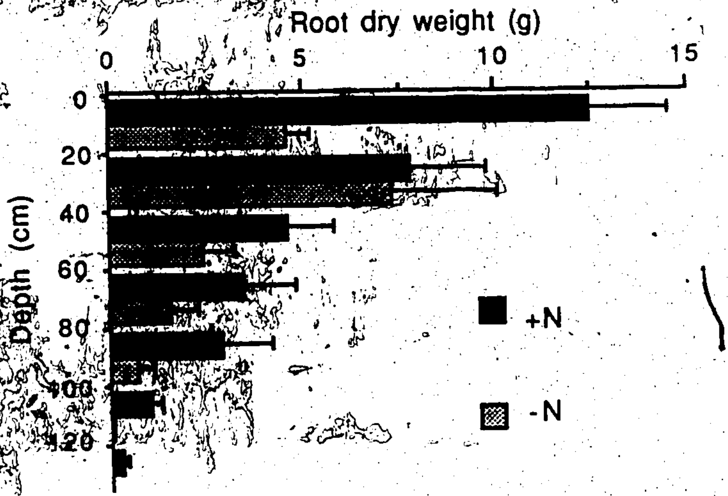
The methodology used for root excavation was the same as for the descriptive study of an established stand in Section 5.1.1 (Figure 4). The root system was sampled to measure root length, root dry weight, and number of root buds. In subsequent trials, the potential of these buds to develop into shoots was determined. Roots present in each 20-cm soil band studied were not divided into root diameter categories since their diameters were very similar within each band, except the top 20-cm band, in which both very fine and very lignified roots coexisted. In general, root diameter tended to decrease with depth.

No underground shoots were observed. This was expected, since the stands were excavated at the early flowering stage, at a time when shoot initiation and growth is slow (Alberta Agriculture, 1984; Hodgson, 1968; Hunter, 1973). Root length in treated stands was nearly twice as high as in the untreated stands in the top 20 cm of soil (Figure 21). No difference was observed between treated and untreated stands below 20 cm depth. For both treated and untreated stands, about a third to a fourth of the root length was in the top 20 cm of soil, respectively. The majority of the root system was, therefore, below the top 20 cm of soil. The highest concentration of root length was in the top 20 cm for the treated stands and between 0 and 40 cm for the untreated stands. Root length decreased with increasing depth below 20 cm for treated stands, and below 40 cm for untreated stands. The depth of penetration of the one-year old stand was 1.4 m (Figures 21 and 22).



% -N	% +N
25.7	34.5
31.3	21.4
21.9	18.2
12.7	12.9
6.3	8.7
1.9	4.5
0.2	2.2

Figure 21. Average root length down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1985. The data represent the means for the roots found in twelve 2 m wide by 10 cm thick by 20 cm deep soil bands. Horizontal lines indicate standard errors for the means for each depth. The percentage distribution of the parameter down the soil profile is tabulated in the columns.



% -N	% +N
33.1	41.5
44.3	23.5
15.0	14.6
7.9	9.1
4.0	7.4
0.4	2.8
0	0.9

Figure 22. Average root dry weight down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1985. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21 for more details.

Root dry weight in the top 20 cm of soil was nearly three times as high in treated stands as in untreated stands (Figure 22). No difference between treated and untreated stands was observed below this level. About a third of the root dry weight was in the top 20 cm of soil for both treated and untreated stands. As for root length, the majority of the root dry weight was below the top 20 cm of soil (Figure 22). The highest concentration of the root dry weight was in the top 20 cm for the treated stands and between 20 and 40 cm for the untreated stands. Root dry weight decreased with increasing depth below 20 cm and 40 cm for treated and untreated stands, respectively.

Close to twice as many emerged root buds were present in the top 20 cm of soil in nitrogen-treated stands as in untreated stands (Figure 23a). No difference between treated and untreated stands was observed below the top 20 cm of soil. The majority of the emerged root buds were in the top 20 cm of soil for treated stands, and in the top 40 cm for untreated stands. Their number declined sharply with depth. Emerged root buds were observed down to 80 cm (Figure 23).

The number of emerged root buds per meter of root was 40% higher in the top 20 cm for treated stands than for untreated stands (Figure 23b), but was 60% lower for treated stands than for untreated stands between 20 and 40 cm depth. The highest number of emerged root buds per meter of root was produced in the top 20 cm of soil for treated stands and in the top 40 cm for the untreated stands. Their number declined more sharply for treated stands than for untreated stands with increasing depth (Figure 23b).

The number of non-emerged root buds in the top 40 cm of soil was twice as high for treated stands as for untreated stands (Figure 24a). The majority of the non-emerged root buds were in the top 20 cm of soil for both treated and untreated stands, and the number of buds declined sharply with increasing depth. Non-

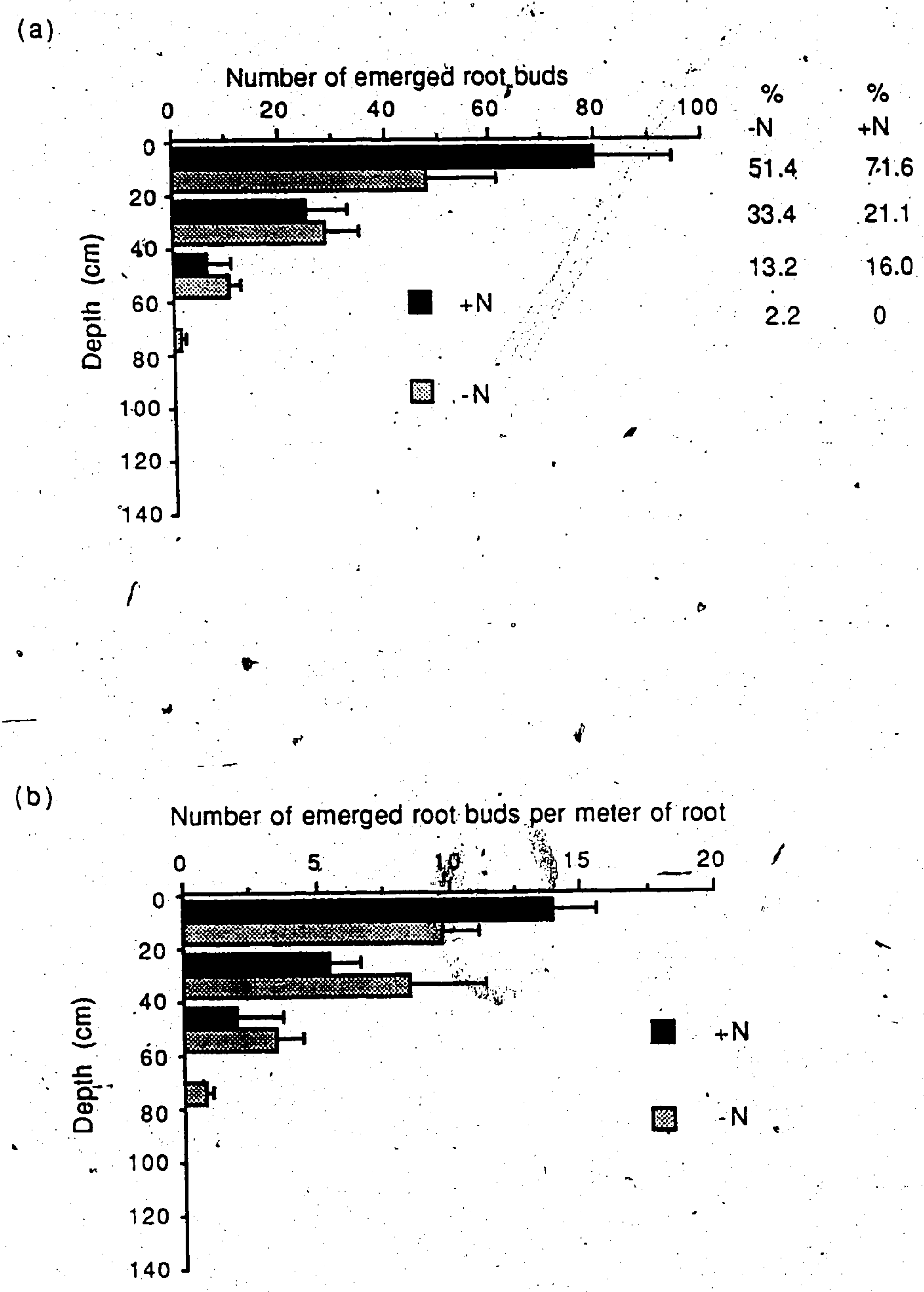
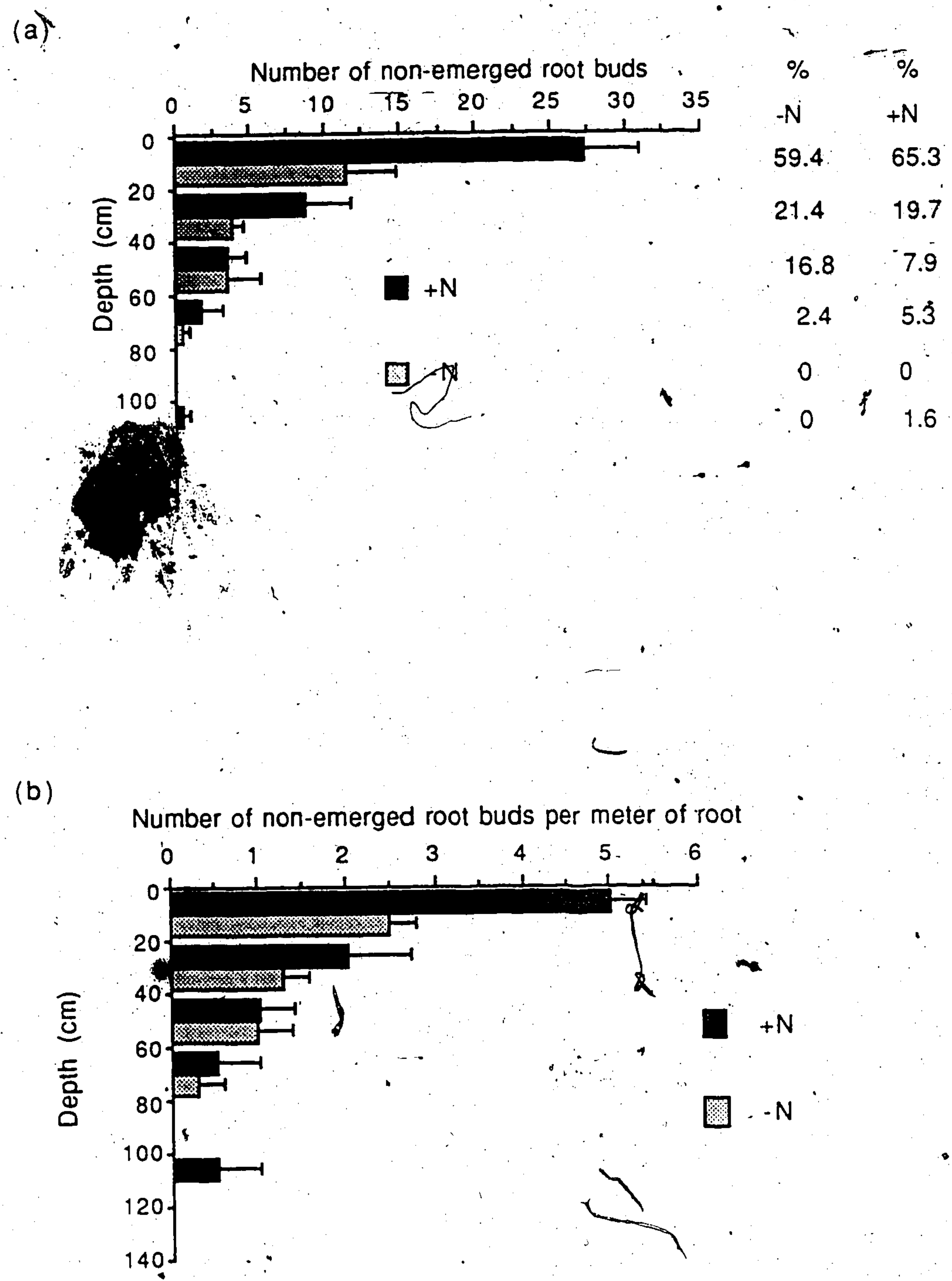


Figure 23. Average numbers of emerged root buds (a) and emerged root buds per meter of root down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1985. The data represent the means for the roots found in four 2 m-wide by 10 cm thick by 20 cm deep soilbands. See Figure 21, page 88 for more details.



% -N	% +N
59.4	65.3
21.4	19.7
16.8	7.9
2.4	5.3
0	0
0	1.6

Figure 24. Average numbers of non-emerged root buds (a) and non-emerged root buds per meter of root (b) down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1985. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

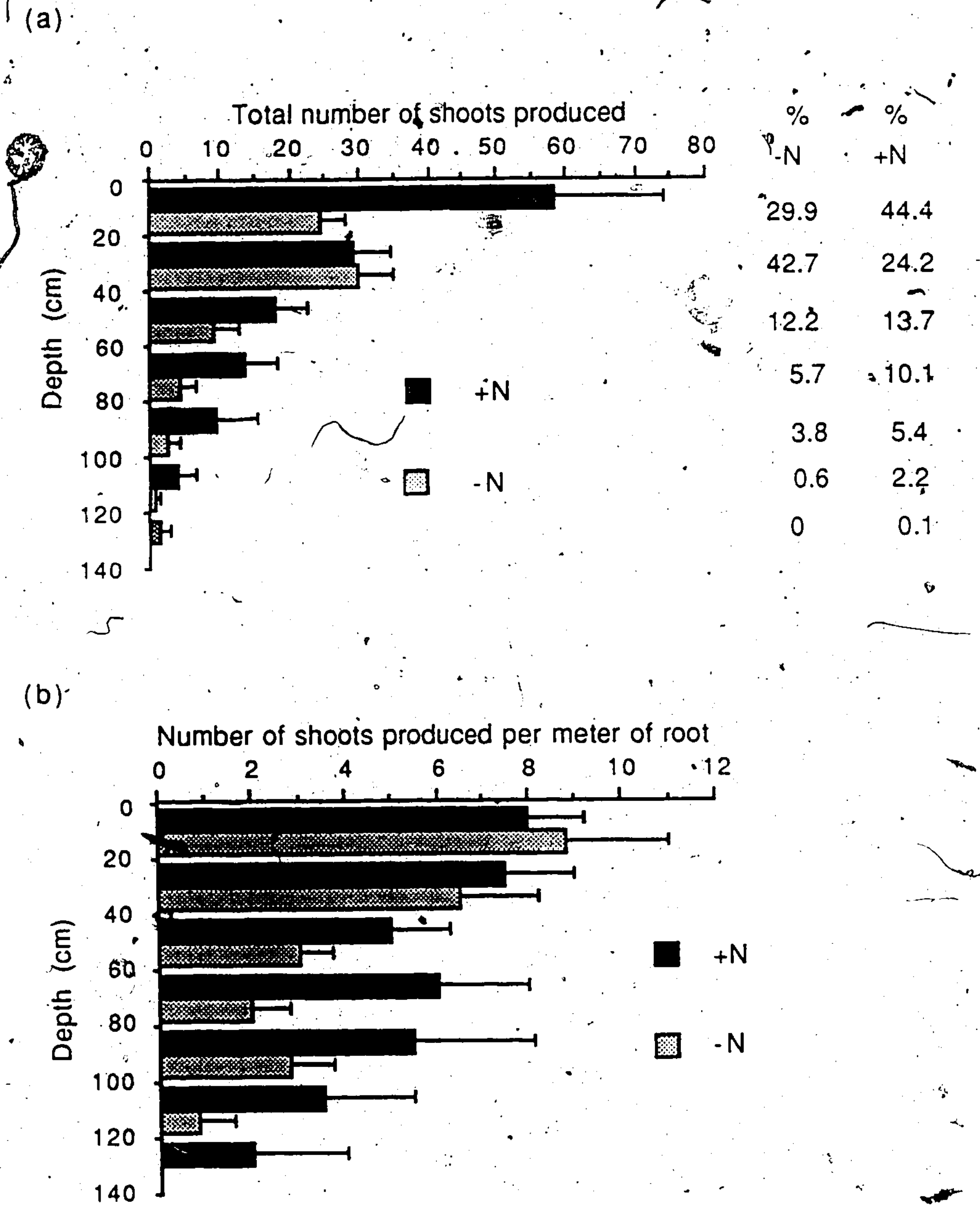
emerged root buds could be detected down into the soil profile to a depth of 120 cm for nitrogen treated stands and to 80 cm for untreated stands (Figure 24).

The number of non-emerged root buds per meter of root in the top 20 cm of soil was twice as high in the treated stands as in untreated stands (Figure 24b). The highest production of non-emerged root buds per meter of root was in the top 20 cm for both treated and untreated stands, and declined sharply with depth.

The shoot production by replanted root pieces from the top 20 cm of soil was higher for treated stands than for untreated stands, and for nearly every 20-cm soil band studied below 40 cm depth (Figure 25a). The highest shoot production was in the top 20 cm for treated stands and in the top 40 cm for untreated stands. The number of shoots produced declined with increasing depth below 20 cm for treated stands and above 40 cm for untreated stands. Shoots were produced from replanted roots sampled at all depths.

The number of shoots produced per meter of replanted root in the top 40 cm of soil did not differ between treated and untreated stands but, below the top 40 cm, treated stands produced more shoots per meter of root than untreated stands (Figure 25b). The highest number of shoots produced per meter of replanted root was in the top 100 cm of soil for treated stands and in the top 40 cm of soil for untreated stands. Their number declined more sharply for untreated stands than for treated stands with increasing depth. Weighted averages of shoot counts in treated and untreated stands were 5 and 4 shoots per meter of root, respectively.

The higher number of aboveground shoots associated with the nitrogen-treated stands (Figures 12, 13, and 16, 17 and 18; Table 10) seems to be more the result of an increase in root length, and thus the result of an increase in total root buds and in shoot production rather than of an increase in root buds or shoot



% -N	% +N
29.9	44.4
42.7	24.2
12.2	13.7
5.7	10.1
3.8	5.4
0.6	2.2
0	0.1

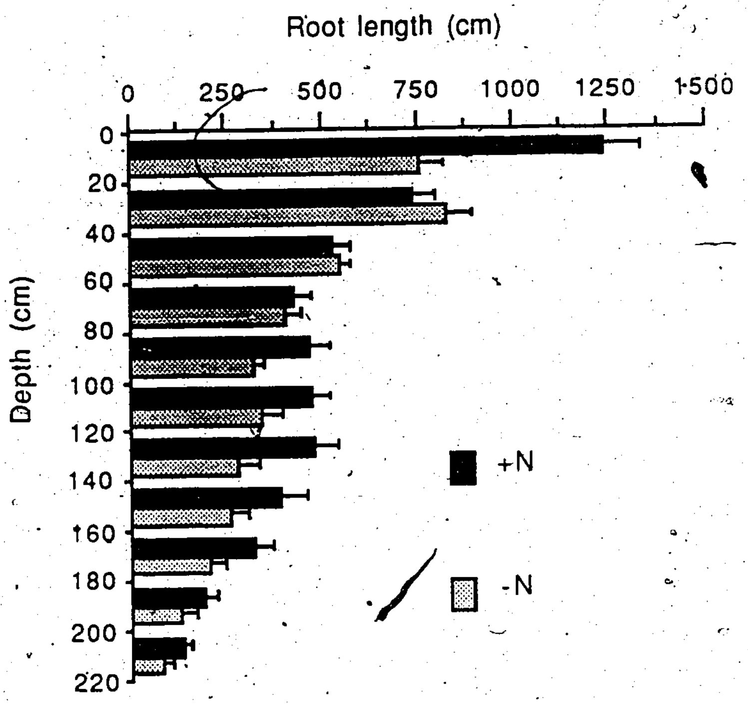
Figure 25. Average values for shoot production (a) and shoot production per meter of root (b) down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands ~~in 1985.~~ The data represent the means for the roots found in four 2 m wide by 10 ~~cm thick~~ by 20 cm deep soil bands. See Figure 21, page 88 for more details.

production per meter of root (Figures 21 to 25).

Similar measurements to those for the 1-year old stands were taken in 2-year old stands. Just prior to excavation of these stands, treated Canada thistle had produced 158 g/m^2 of shoot dry matter, corresponding to 15 shoots/ m^2, and the untreated stands had produced 149 g/m^2 or 13 shoots/m^2.

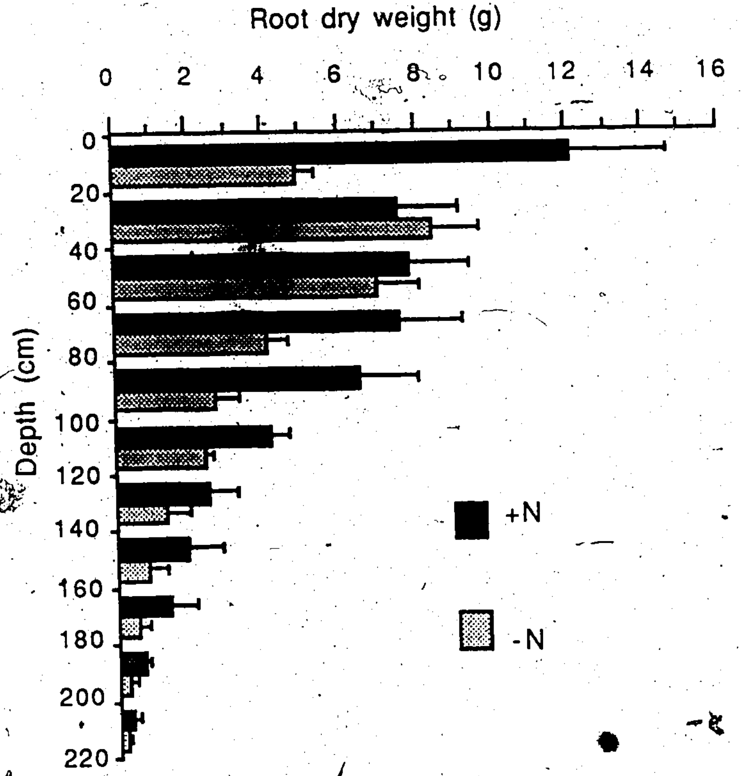
The root length in the top 20 cm of soil was 75% higher in treated stands than in untreated stands (Figure 26). No difference was observed between treated and untreated stands below the top 20 cm of soil. For both treated and untreated stands, about a fifth of the root length was in the top 20 cm of soil and, therefore, the majority of the root length was below the top 20 cm of soil. The highest concentration of root length per unit soil volume was in the top 20 cm of soil for treated stands, and between 0 and 40 cm depth for untreated stands. Root length declined with increasing depth below 20 cm for treated stands and below 40 cm for untreated stands. The root system of the two-year old stands reached 220 cm in depth (Figures 26 and 27).

Treated stands had 2.5 times as much root dry matter in the top 20 cm of soil as the untreated stands (Figure 27). No difference between treated and untreated stands was observed below the top 20 cm of soil, for every 20-cm soil band, with the exception of the depths between 60 and 100 cm, in which twice as much dry weight was produced in treated stands as in untreated stands. About a sixth and a fourth of the root dry weight was in the top 20 cm of soil, for both treated and untreated stands, respectively, and therefore, the majority of the root dry weight occurred below the top 20 cm of soil. The highest concentration of the root dry weight per soil volume was in the top 20 cm of soil in treated stands, and between 20 and 100 cm depth in untreated stands. The concentration of root dry weight decreased with increasing depth.



% -N	% +N
19.0	23.7
21.0	14.1
13.7	10.3
9.8	7.9
7.8	8.4
7.9	8.7
6.4	8.6
5.7	6.7
4.4	5.7
2.8	3.4
1.5	2.4

Figure 26. Average root length down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent ~~the means~~ for the roots found in twelve 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.



% -N	% +N
15.9	23.2
26.3	14.7
21.9	15.5
12.6	14.4
7.9	12.5
6.7	8.1
3.5	4.6
2.4	3.1
1.5	2.2
0.9	1.2
0.5	0.7

Figure 27. Average dry weight down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

From visual observation, roots appeared to be much finer in the top 20 cm of soil in the two-year old stands than in the 1-year old stands. Evidence to support this observation lies in the fact that the root length measured for the top 20-cm soil band in the 2-year old stands was about twice as high as the root length measured in the 1-year old stands (Figures 21 and 26), while the root dry weights of the stands were similar (Figures 22 and 27).

No difference in the number of underground shoots was observed between treated and untreated stands (Figure 28a). The number of underground shoots was highest in the top 20 cm of soil, and declined with increasing depth. They were present down to a depth of 60 cm (Figure 28a).

No difference in number of underground shoots per meter of root was observed (Figure 28b). Their number was highest in the top 20 cm of soil, and declined with increasing depth.

Many more underground shoots were observed in the 2-year old stands than in the 1-year old stands or the established stand excavated in 1984. The high precipitation early in the growing season may have promoted the release of root bud dormancy independent of the plant's growth stage (Appendix 8). Furthermore, the excavation date in 1986 was earlier than in 1984 or 1985, and even though the excavations of the three years were done at the same growth stage of aboveground shoots, it is possible that the growth stage of the plant parts below the soil surface would not have been the same.

There were twice as many emerged root buds in the top 20 cm of soil in treated stands as in untreated stands, but no difference between treated and untreated stands was observed at greater soil depths (Figure 29a). The majority of the emerged root buds were in the top 20 cm of soil in both treated and untreated stands, and their number declined with increasing depth. Emerged root buds were

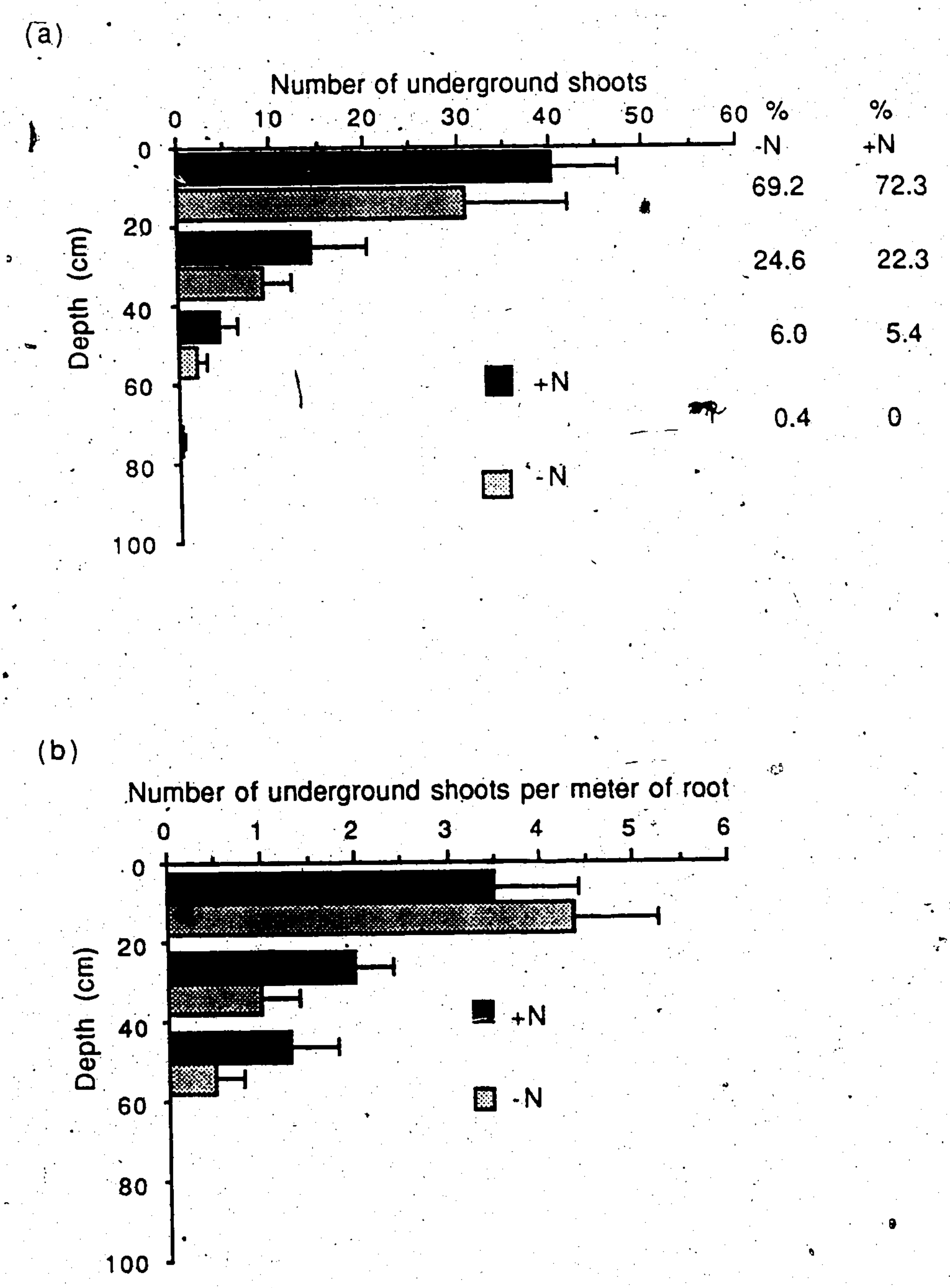


Figure 28. Average numbers of underground shoots (a) and underground shoots per meter of root (b) down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

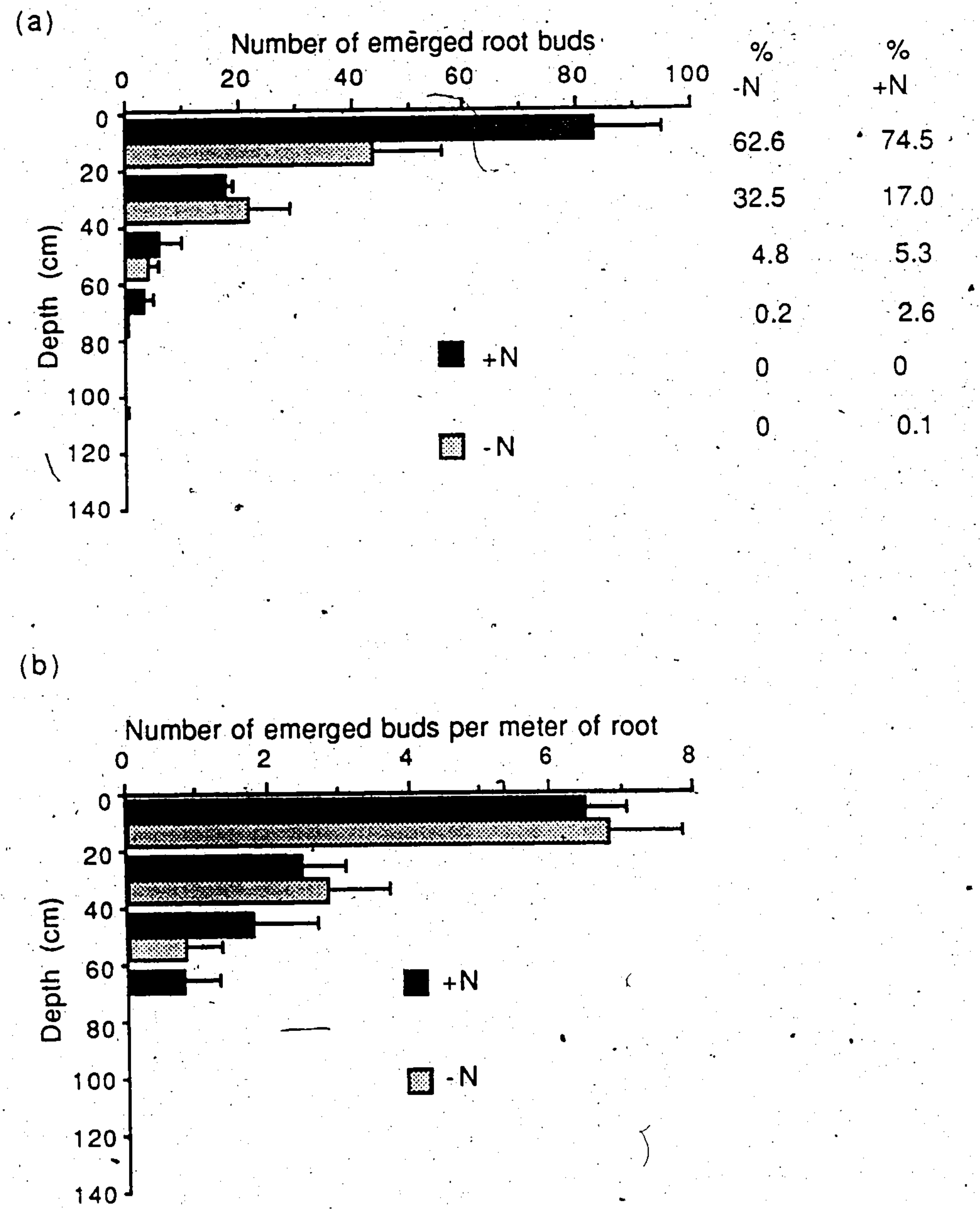


Figure 29. Average numbers of emerged root buds (a) and emerged root buds per meter of root (b) down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

observed down to 120 cm (Figure 29).

No difference was observed between the number of emerged root buds per meter of root in treated and untreated stands (Figure 29b). The highest number of emerged root buds produced per meter of root was in the top 20 cm of soil. The number of root buds per meter of root declined with increasing depth.

The total numbers of emerged root buds counted for each 20-cm soil band in the 2-year old stands were very similar to those counted in the 1-year old stands (Figures 23a and 29a). However, the number of emerged root buds per meter of root was about half that in the one-year old stand (Figures 23b and 29b). It can be speculated that the finer roots present in the top 20 cm of soil of the 2-year old stands compared to the 1-year old stands were incapable of supporting the production of buds.

About twice as many non-emerged root buds were present in the treated stands as in the untreated stands in the top 40 cm of soil (Figure 30a), but no difference between stands was observed below that depth. The majority of the non-emerged root buds were in the top 20 cm of soil for both treated and untreated stands, and the numbers declined with increasing depth. Non-emerged root buds were present down to 120 cm (Figure 30).

There were more than twice as many non-emerged root buds per meter of root in treated stands as in untreated stands for roots sampled at depths between 20 and 40 cm and depths between 60 and 80 cm (Figure 30b), but there was no difference in number of non-emerged root buds per meter of root between treated and untreated stands at any other depths. The highest number of non-emerged root buds per meter of root was in the top 40 cm of soil for treated stands and in the top 20 cm of soil for untreated stands. Their number per meter of root declined with increasing depth.

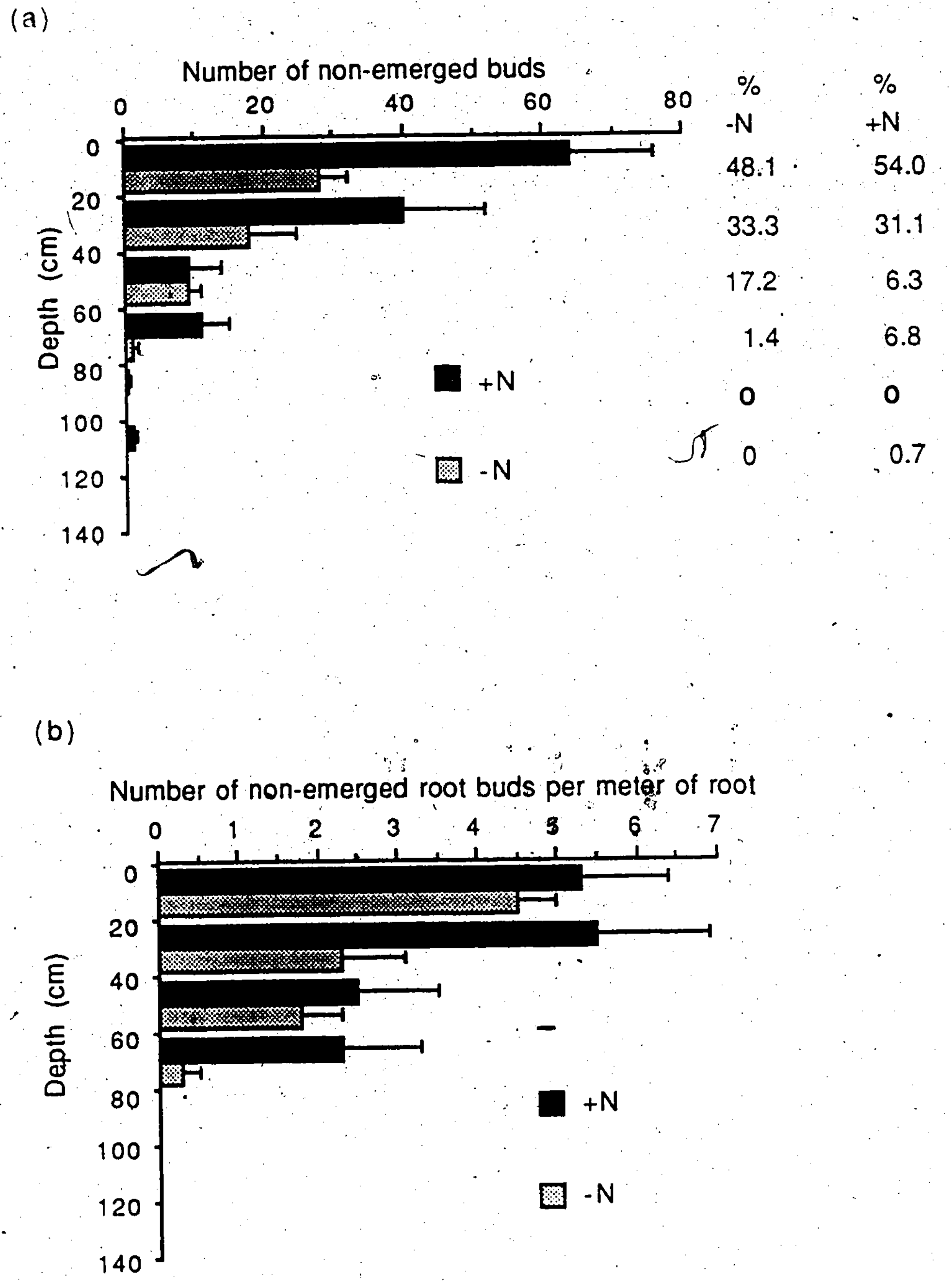


Figure 30. Average numbers of non-emerged root buds (a) and non-emerged root buds per meter of root (b) down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

More non-emerged root buds were present in the 2-year old stand than in the 1-year old stand for every 20-cm soil band examined down to 120 cm (Figures 24a and 30a). Furthermore, a higher proportion of the total number of non-emerged root buds was present below the top 20 cm of soil in the 2-year old stand than in the 1-year old stand. On average, 38% and 49% of the non-emerged root buds were located below the top 20 cm in the one and two-year old stands, respectively (Figures 24a and 30a).

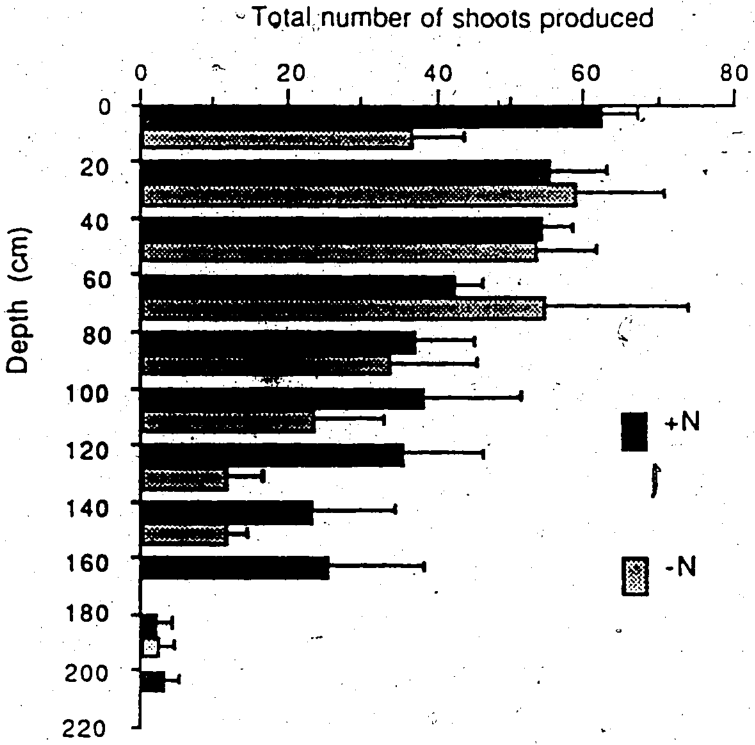
The number of shoots produced by planting root fragments collected in the nitrogen-treated stands was much higher than for roots from the untreated stands, in the top 20 cm of soil, and below 100 cm (Figure 31a). The majority of the shoots were produced by roots sampled in the top 60 cm of soil for treated stands and by roots sampled between 0 and 80 cm for untreated stands. The number of shoots produced declined with increasing depth, the rate of decline being greater in untreated stands. Shoots were produced from replanted roots sampled at all depths (Figure 31).

The number of shoots produced per meter of replanted root was similar for treated and untreated stands, and was highest between 20 and 100 cm depth (Figure 31b). The number of shoots produced per meter declined on roots sampled above and below these depths. The weighted average number of shoots produced per meter of replanted root was six for both treated and untreated stands.

There was no difference in the nitrogen level of the shoots or roots between treated and untreated stands (Table 21). No relationship between nitrogen levels and release of root bud dormancy was observed.

The higher shoot density observed (Figure 16) in treated stands compared to untreated stands seemed to be associated with the higher proportion of roots close to the soil surface. There was no strong evidence of any release of root bud

(a)



% -N	% +N
16.3	17.3
21.2	15.1
19.7	15.9
17.1	12.9
11.0	10.4
6.9	9.4
3.7	8.6
3.6	5.5
0	5.2
0.5	0.4
0	0.7

Figure 31a. Average values for shoot production down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

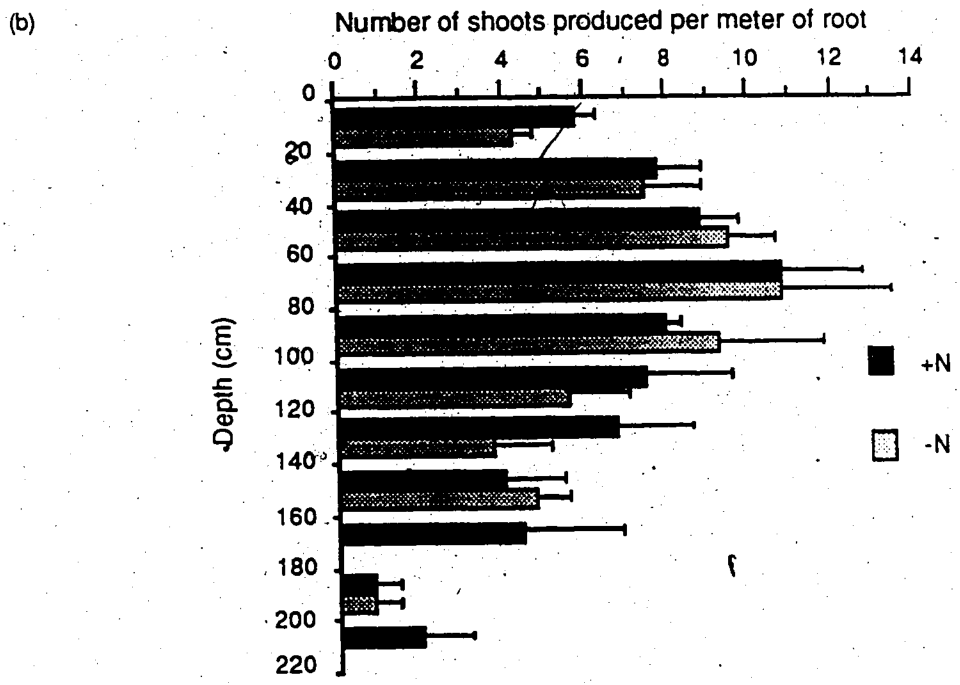


Figure 31b. Average values for shoot production per meter of root down the soil profile of nitrogen-treated (+N) and untreated (-N) Canada thistle stands in 1986. The data represent the means for the roots found in four 2 m wide by 10 cm thick by 20 cm deep soil bands. See Figure 21, page 88 for more details.

Table 21. Nitrogen content of shoots and roots of Canada thistle plants grown under two soil nitrogen levels excavated at Michener Park in 1986.

	Nitrogen Content		
	Nitrogen Applied		
Depth	0 kg/ha	100 kg/ha	P^a
(cm)	(%)	(%)	
	Aboveground Shoots		
	4.1	3.7	0.29
	Underground shoots		
0-20	0.6	0.5	0.65
20-40	0.4	0.7	0.33
40-60	0.4	0.2	0.42
60-80	0.2	0.0	0.35
	Roots		
0-20	2.2	1.8	0.07
20-40	2.0	1.9	0.38
40-60	2.1	2.0	0.51
60-80	2.0	2.1	0.83
80-100	1.9	2.1	0.07
100-120	1.9	2.3	0.21
120-140	2.1	2.5	0.34
140-160	2.5	2.7	0.80
160-180	2.2	2.8	0.36
180-200	2.9	2.9	0.99
200-220	2.1	1.6	0.71

[a] Level of significance based on a two-tailed t-test.

dormancy.

4.4 General Discussion

In the experiment in which nutrient solution was used as a growth medium, nitrogen in trials 1 and 2 affected root bud dormancy differently. In trial 1 (Tables 5 and 6), the high nitrogen level resulted in an increase in emerged and non-emerged root buds per meter of root compared to the low nitrogen level. These results support McIntyre and Hunter's (1975) conclusion that nitrogen does release root bud dormancy. However, the results reported here show that the production of non-emerged root buds was increased in response to 210 ppm nitrogen level compared to 21 ppm nitrogen level, while McIntyre and Hunter (1975) reported an increase in the production of non-emerged root buds in response to nitrogen.

At the 17 to 21-leaf stage, the plants were still vegetative with no shoot bud formation, under the above noted growth room conditions. At that time, carbohydrate partitioning would be in favor of shoot growth rather than of root growth (Arny, 1932; Hodgson, 1968; Welton et al., 1929). The observations obtained for Canada thistle plants growing under 150 $\mu E^{-1}.m^{-2}.sec^{-1}$ can be explained in two ways. Firstly, a low root carbohydrate level, coupled with 210 ppm nitrogen in the growth medium would have resulted in a higher root bud growth than with 21 ppm nitrogen. This is in support of observations made by Buchholtz (1962), where new shoots occurred on rhizomes of quackgrasss only with a low carbohydrate:nitrogen ratio. Secondly, plants growing under 21 ppm nitrogen had inadequate levels of assimilates resulting in reduced root growth and root bud initiation and growth compared to plants growing under 210 ppm.

In the second trial (Tables 7 and 8), in which Canada thistle was grown under 250 $\mu E.m^{-2}.sec^{-1}$, a higher number of aboveground shoots was produced at a low nitrogen level than at a high nitrogen level. This result does not support Hamdoun's (1970) findings, where root fragments and seeds were used to generate plants, or McIntyre and Hunter's (1975) findings, where seedlings were used. However, the results reported here do support some of Hoefer's (1981) findings, where root fragments were used to generate new plants, but not when he used seedlings. Unfortunately, the light intensity used was not mentioned in Hamdoun's paper, and it was defined in lux in Hoefer's or McIntyre and Hunter's papers. However, one could estimate an intensity of about 350 $\mu E.m^{-2}.sec^{-1}$.

The observations obtained for Canada thistle plants growing under 250 $\mu E^{-1}.m^{-2}.sec^{-1}$ could also be explained in two ways. Firstly, shoots growing under 210 ppm nitrogen could have been able to translocate more carbohydrates to the root system than shoots growing under 21 ppm. The resulting carbohydrate:nitrogen ratio might have been too high to promote root bud growth. Shoots growing under 210 ppm could also have been able to translocate more growth inhibitors, as auxins, than shoots growing under 21 ppm. Secondly, shoots already present in the 210 ppm growth medium could have competed with new shoots for nutrients better than shoots growing under 21 ppm nitrogen.

The ability of Canada thistle to alter its morphology in response to environmental conditions is remarkable. The use of a single clone for all experiments minimized the amount of variation, but still did not produce consistent results.

Various studies have suggested a trade-off between plasticity and genetic variation (Schlichting, 1986), implying that species which produce large numbers of seed generally produce individuals that do not adjust well to variations in environmental conditions. Canada thistle would be a good example in support of these suggestions, considering that genetic variation is not a major characteristic of the survival strategies of the species. In fact, seeds have been reported by Bakker (1960) and Detmers (1927) to be inefficient in getting new stands established, while any root piece would produce shoots and roots in nearly any environment.

Shoot production of Canada thistle under field conditions in Alberta was affected by nitrogen treatments, with nitrogen-treated plots having a higher shoot density than untreated plots in most cases (Figures 12 to 18; Table 10). The exception occurred on plots in 11 and 12-year old stands, where some nitrogen-treated plots had a lower shoot density than untreated plots (Table 10). This exception could be related to the decreasing photoperiod and prevailing high relative humidity at the time of treatment (Appendix 8), although any inference on how this interaction occurred would be difficult.

From the fact that nitrogen had significant effects on shoot production under field conditions, while no conclusive effects were observed under growth room conditions, it became obvious that it is very difficult to extrapolate from growth room conditions to field conditions.

In Experiments 1 and 2 (Tables 11 to 20), in which Canada thistle plants were exposed to two nitrogen levels between the 5th and 13th week after planting a root fragment, or up to the early flowering stage, and between the 5th and 17th week after planting, there were few differences between nitrogen-treated plants and untreated plants.

One characteristic of the data of Experiments 1 and 2 was that the probabilities of finding differences in root length, root dry weight, number of root buds and shoot production of large roots between treated and untreated plants were always higher for large roots than for the same types of measurements taken on medium or small roots. The large roots with secondary thickening being the oldest and, therefore, the ones that were exposed the longest to the different nitrogen levels between treated and untreated plants, it was not surprising to find that these large roots were more responsive to the nitrogen treatment than unlignified roots.

For both Experiments 1 and 2, other environmental conditions had a greater effect on Canada thistle plants than nitrogen fertilization alone. In experiment 1 (Tables 11 to 15), the major differences in environmental conditions between the two trials might have been temperature and soil water content with the plants in the outdoor trial being exposed to much lower temperatures and wetter conditions than those in the indoor trial. The outdoor trial could have resulted in a much higher production of underground shoots and emerged and non-emerged root buds per meter of root than the indoor trial. Hoefer (1981) reported that established Canada thistle stands grown in a sand-soil mixture under a 15-hour photoperiod at 15/5°C day/night temperature produced significantly more root buds than at 25/15°C . He explained that the transport of assimilates to roots could occur readily if respiration and transpiration were low. The wetter conditions of the outdoor trial compared to the indoor trial could also have affected the root bud production. High relative humidity has been reported to release root bud dormancy of Canada thistle (Hunter et al., 1985), and evidence for water as a factor involved in root bud initiation and growth has been provided for leafy spurge (McIntyre, 1979) and milkweed (Hsiao and McIntyre, 1984).

In Experiment 2, the major difference in environmental conditions was the low precipitation in the 1985 trial compared to the 1986 trial (Appendix 8). In 1985, there was a higher number of emerged root buds per meter of root, a lower number of non-emerged root buds per meter of root and a lower production of shoots on root pieces per meter of root than in 1986. As mentioned earlier, high relative humidity or water has been reported to release root bud dormancy of some weed species.

These results might suggest that there should have been a lower number of emerged root buds per meter of root in 1985 instead of in 1986. It was therefore very difficult to explain how the level of precipitation alone could have had the effects reported here. Precipitation probably interacted with various other unidentified factors that varied between the two years of study.

In Experiment 2 (Tables 16 to 20), the number of root buds from the large root diameter category did not correspond as well to the shoot production by the same diameter category as did root bud numbers from the medium and small diameter categories. Since the lignified, oldest roots were generally closer to the shoots than medium or small roots, the shoots probably had a more direct influence on their root bud initiation and growth, and thus, shoot production. Cutting shoots from roots probably had more influence on the regenerative capacity of roots for shoot production, than did removal of shoots from medium and small roots.

The outdoor trial of Experiment 1, done in 1986, and the 1986 trial of Experiment 2 gave different results. In trial 1 of Experiment 1, more emerged and non-emerged root buds per meter of large roots were counted on nitrogen-fertilized plants than on untreated plants, while in trial 2 of Experiment 2, more emerged root buds per meter of large root were counted on treated plants than on untreated plants. No difference was observed for non-emerged buds between treated and untreated plants. It is possible that, a certain time after the application of nitrogen, the soil nitrogen was decreased by leaching or by uptake by Canada thistle or various soil microorganisms, and that the reduced amount of nitrogen did not affect root bud production.

The "intensity" of root bud dormancy at different growth stages of Canada thistle affected the proportion of underground shoots, emerged and non-emerged root buds. Low numbers of underground shoots and emerged root buds would be expected at growth stages occurring after the early bud stage, considering that the inhibition of shoot production was reported to be greatest after the bud stage, under summer conditions similar to the ones found in Alberta (Alberta Agriculture, 1984; Hodgson, 1968; Hunter, 1973).

The effects of nitrogen on Canada thistle stands excavated 1 and 2 years after establishment were clear cut (Figures 21 to 31). The young stands studied were the same as the ones used in the experiment examining the effects of nitrogen on the shoot production of Canada thistle. From the excavation of the stands, the increase in shoot production and density from nitrogen treatment compared to no treatment was associated with an increase in root growth in the top 20 cm of soil.

In the 1-year old stand, the number of emerged root buds per meter of root was highest near the soil surface in the treated stands rather than being more evenly distributed in the top 80 cm of soil of untreated stands (Figure 23). However, in the 1-year old stands, nitrogen treatment promoted a higher shoot production on root fragments sampled deep into the soil. In the 2-year old stands, nitrogen treatment resulted in a more even distribution of underground shoots per meter of root in the top 60 cm of soil. In addition to supporting the fact that there was no relationship between the number of root buds observed in the soil profile and the regenerative capacity of the root system, these observations support the conclusion that nitrogen treatment had the potential of increasing the severity of a Canada thistle problem.

Cultivation of the top 20 cm of soil would affect a higher percentage of the root system growing in nitrogen-treated plots compared to untreated plots. However, the same mass and length of roots would be left below the cultivated zone in both treated and untreated stands, with the shoot growth potential of roots of nitrogen-treated stands sometimes being higher than for roots of untreated stands, as was observed for the 1-year old Canada thistle. Furthermore, the number of underground shoots per meter of root below the top 20 cm of soil was higher in treated stands than in untreated stands, as in the 2-year old Canada thistle stands. It would take approximately the same time for mechanical control methods to starve the root system of a treated and untreated stand, but the potential for infestation of the roots below the top 20 cm of soil would be greater for treated than for untreated stands. Cultivation, if not well-timed, could even increase the severity of the Canada thistle problem in treated stands since more roots would be dispersed throughout the field in treated stands than in untreated stands.

In all experiments in which the nitrogen content of different plant parts of Canada thistle was determined, the nitrogen content of plants subjected to different nitrogen levels in their growth medium was not correlated to any observed effects of nitrogen on root bud dormancy. One reason might be that nitrogen-treated plants were affected by nitrogen only to the extent their biomass was increased in adjustment to a new nitrogen level.

From the study on the effects of nitrogen on Canada thistle under field conditions, nitrogen could have an effect on root bud dormancy, but there could be many interactions with abiotic factors which made any predictability of the nitrogen effects very difficult. Because of all the possible interactions, it is unlikely that nitrogen could affect herbicide efficacy in any consistent way by releasing root bud dormancy.

The descriptive aspect of Canada thistle growth in this study shows that shoot production over time in 1984 (Figure 12) was represented by a sigmoid curve. One could argue that the curves represented a typical logistic growth curve. Population growth curves are normally sigmoid, and it is common to find that the good fit of a logistic curve is more apparent than real. To draw the conclusion that the growth of a particular population is logistic, abiotic environmental factors should be sufficiently constant not to affect the birth and death rate, and crowding should affect all members of the population equally (Pielou, 1977). These conditions were not met, and no conclusion can be drawn about the type of growth of the population.

The rate of expansion was as much as 0.95 cm/day between 5 and 13 weeks after planting a root fragment (Tables 3 and 4). The low rate observed in the early stage of growth of Canada thistle was consistent with the fact that the plants did not produce secondary shoots before 4 weeks after planting and after the initial sprouting in 1984 and 1985, respectively (Figures 12 and 13). Rate of expansion would increase with time, though, when the increasing amount of aboveground biomass would increase the production of photosynthate translocated to the root system. From these data, the root system of the established stand studied at the Ellerslie Research Station in 1984 would have taken only 2 years to reach a depth of 2 m.

A notable feature of the plants in Experiments 1 and 2 (Tables 11 to 20) was the lower production of emerged and non-emerged root buds per meter of roots in Experiment 2 than in Experiment 1. The more numerous shoots harvested 18 weeks after planting a root fragment (Experiment 2) could have been able to compete for nutrients more efficiently than the fewer shoots produced by the plants harvested 13 weeks after planting, which resulted in less nutrients for root bud initiation and growth (Experiment 1). Furthermore, the shoots harvested 18 weeks after planting could have had the ability to produce and translocate growth inhibitors better than the younger shoots. Of course, one cannot ignore the prevailing environmental conditions to which these plants were exposed. Under different conditions, it would be possible that different trends might occur.

The data of the trials of Experiments 1 and 2, done in 1986 (Tables 11, 12, 18 and 19), in which plants were harvested 13 and 18 weeks after root fragments were planted, could be used to calculate growth rates of Canada thistle. During 6 weeks, from July 16 to August 26, 6 g of aboveground shoot dry matter was produced per day, at least 3 g of root dry matter per day, and at least 2 cm of roots with a diameter larger than 0.5 mm per day. The root system of a plant harvested 18 weeks after a 10-cm long root fragment was planted had the potential of producing 903 shoots when cut into 10-cm long pieces.

From the data obtained on shoot density and the root system of Canada thistle stands, it became obvious that one cannot make predictions about root systems just by looking at the aboveground shoots (Figures 5 to 8, and 21 to 31). For example, the 10-year old stand studied at the Ellerslie Research Station in 1984, that had been cultivated repeatedly throughout the years, had a shoot density (40 shoots/m^2) which was more than twice the shoot density of a 2-year old undisturbed Canada thistle stand (15 shoots/m^2). However, the root system of the 10-year old site was only about half as extensive in terms of root length and root dry weight as the root system of 2-year old stands.

The majority of the root biomass was below the top 20 cm of soil (Figures 5, 6, 21, 22, 26, 27). In the 1-year old stands, an average of 37% of the root dry weight would be affected by cultivating the top 20 cm of soil, compared to 20% for the 2-year old stands and 29% for the 10-year old stand. Well-timed cultivation would starve the root system, but the starvation process would be rather slow, especially for the undisturbed 2-year old stands.

The depth reached by the root system of the 10 year old stand and the 2-year old stand was about 2 m. This depth was reported to be common for Canada thistle

(Hunter, 1985; Pavlychenko, 1943), as well as for other perennial weeds, such as poverty weed (Pavlychenko, 1943).

The number of root buds produced per meter of root for the 10-year old stand was twice as high as the number produced in the one and 2-year old stands (Figures 7, 22, 23, 28, 29). There were also about twice as many non-emerged root buds per meter of root in the 2-year old stands as in the 1-year old stands. This suggests that there is an increase in number of root buds produced per meter of root as a stand ages.

The depths from which roots were sampled had little effect on their regenerative capacity for the production of shoots. By comparing the data for shoot production of root pieces of the 10-year old stands (Figure 25) to the corresponding data of the 1 or the 2-year old stands (Figure 31), it was apparent that there was a tendency for more consistent shoot production with increasing depth. In the 10-year old stand, a weighted average of eight shoots per meter of root was obtained. One could speculate that this value would be attained with time by the newly established stands.

There was no correlation between root bud production and shoot production of root fragments. There were more root buds closer to the soil surface than the values obtained for shoot growth potential, and there were fewer root buds produced deeper into the soil than there were shoots being produced by root fragments. The inhibition of root bud growth close to the soil surface could have been caused by the competition for nutrients by the growing shoots, or by growth inhibitors produced by the growing shoots and translocated to the root buds, or by growth inhibitors produced by the buds or the root system. Environmental conditions close to the soil surface such as higher temperatures or light intensity or lower soil moisture compared to deeper into the soil could also have inhibited root bud growth, but no evidence supporting their involvement was available.

In contrast, the roots sampled deeper into the soil produced more shoots than the actual number of root buds present at sampling time. Three explanations can be given: firstly, environmental factors prevailing close to the soil surface but not deep into the soil were conducive to root bud formation. Two factors that came to mind were light and oxygen. In general though, light has little effect on root bud initiation but marked effects on bud development (Peterson, 1975). As for the effect of oxygen, very little is known. It appears that, at least in quackgrass, oxygen is not involved in prolonged inactivity of vegetative buds, since its effects only occur when its concentration is reduced to 15%, a level found in waterlogged soil (Buchholtz, 1962). Secondly, some factors inhibiting root bud initiation and growth could be present deep into the soil but not close to the soil surface. One could think of a high carbon dioxide concentration as a factor. However, it appears that 10% carbon dioxide or higher is required to reduce root bud activity in quackgrass, which is the extreme limit encountered in soils that are not waterlogged (Buchholtz, 1962). No information is available for Canada thistle. Thirdly, one could speculate that competition and inhibition caused by the rest of the plant above the part of the root system examined could also occur. No evidence supporting the later explanation was available.

The methodologies used in studying Canada thistle were laborious and time-consuming, with the methodology used in the experiment on the rate of expansion of the root system of Canada thistle also being expensive. However, the results obtained using these methodologies represent as accurately as possible the root system of Canada thistle. The major disadvantage of these methodologies was that they were so time-consuming that few replicates could be included.

5. SUMMARY AND CONCLUSIONS

Canada thistle was grown in several different experiments, in nutrient solution and in soil, and under growth room conditions and in the field. Under growth room conditions, the effects of nitrogen at a concentration of 210 ppm compared to 21 ppm on Canada thistle grown in nutrient solution were different under different light intensities. At 150 $\mu E.m^{-2}.sec^{-1}$, nitrogen released root bud dormancy while at 250 $\mu E.m^{-2}.sec^{-1}$ the release of bud dormancy was questionable.

Under field conditions, nitrogen in the form of urea was applied at a rate of 70 kg/ha or 100 kg/ha and incorporated to 10-cm depth. Nitrogen increased shoot production of 1- and 2-year old stands and of most plots on an 11- to 12-year old stand. However, in the 1- and 2-year old stands, the increase in shoot production was associated mainly with an increase in root length and root mass in the top 20 cm, and not with a release of root bud dormancy. The Canada thistle problem in stands that had been treated by nitrogen could then be more severe than in untreated stands. Cultivation of a nitrogen-fertilized stand could result in more roots being spread throughout the field than in the case of an untreated stand.

Nitrogen applied on plots in an established stand did not always result in an increase in shoot production. Furthermore, the response of Canada thistle plants grown in large containers filled with soil in the field or under growth room conditions appeared to have been influenced by other environmental conditions than nitrogen fertilization.

Nitrogen, in the form and at the rates used in this study, did not consistently affect root bud dormancy under field conditions found in Alberta. The fact that root bud dormancy was not unequivocally released implied that the sink size for herbicide translocation would remain relatively unchanged. Consequently, the efficacy of foliage-applied herbicides would not be affected by nitrogen treatment by releasing root bud dormancy.

The average expansion of the root system was estimated as being as high as 0.95 cm/day between 5 and 13 weeks after planting root fragments of Canada thistle under field conditions in Alberta. Seven weeks after planting a root fragment, the rate of expansion was lower than 0.63 cm/day, while 13 weeks after planting, the rate was higher than 0.95 cm/day. It was assumed that when the production of leaves or secondary shoots increased, more photosynthate was produced and available for root growth. Thus, the rate of expansion of the root system might be expected to increase with time.

Between 13 and 18 weeks after root fragments of Canada thistle were planted in 1986, the Canada thistle plants produced 6 g of aboveground shoots per day, and 2 cm of root with a diameter larger than 0.5 mm per day, corresponding to 3 g of root dry matter per day. In 1985 and 1986, the root system of a plant harvested 18 weeks after a root fragment was planted had the potential of producing an average of 903 shoots, if the root system, cut into 10-cm long root pieces, was replanted.

From the observed relationship between shoot density and root system parameters, it is clear that one cannot make inferences about the root system simply by looking at aboveground shoots. For example, a 10-year old site with a density of 40 shoots/m^2 had about half of the root length and root dry weight of a 2-year old stand that had a shoot density of 15 shoots/m^2. However, the number of root buds per meter of root in the 10-year old stand was about twice that in the 2-

year old stand. By comparing the number of root buds from the 1, 2 and 10-year old stands, it was obvious that root buds became more numerous deeper in the soil over time.

Only 20 to 37% of the root dry weight was in the top 20 cm of soil, and therefore only a small portion of the root system would be vulnerable to cultivation. Cultivation could still starve the root system, but starvation should be expected to be slow.

The depth reached by the root system of a 1-year old Canada thistle stand was 1.4 m, of a 2-year old stand 2.2 m and of a 10-year old stand 1.8 m. The greatest depth at which root buds were found was 1.2 m. Nevertheless, roots sampled at any depth, cut and replanted, had the potential of producing shoots. No correlation between the number of root buds observed at a given depth and the regenerative capacity of the roots observed at the same depth was observed.

From a practical point of view, in studying the effects of various compounds on root bud dormancy, little attention should be paid to the effects of compounds on the number of root buds present, but rather, attention should be given to the number of shoots produced after planting root fragments. One should be aware of all the possible interactions that a compound could have with various abiotic and biotic factors influencing the root bud dormancy of the species.

BIBLIOGRAPHY

Adams, B.W. 1983. The effect of mowing on western snowberry. M.Sc. thesis. University of Alberta. 120 pp.

Alberta Agriculture. 1984. Canada Thistle, its Biology and Control. Agdex 641-5. 5 pp.

Amor, R.L. and R.V. Harris. 1974. Distribution and seed production of *Cirsium arvense* (L.) Scop. in Victoria, Australia. Weed Res. 14: 317-323.

Arny, A.C. 1932. Variations in the organic reserves in underground parts of five perennial weeds from late April to November. Univ. of Minnesota. Agr. Exp. Stat. Tech. Bull. 84:1-28.

Aspinall, D. 1961. The control of tillering in the barley plant. 1. The pattern of tillering and its relation to nutrient supply. Austr. J. Biol. Sci. 14:493-505.

Bakker, D. 1960. A comparative life history of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. Pages 205-222 *in* J.L. Harper ed., The Biology of Weeds: A Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Bendall, G.M. 1975. The allelopathic activity of Californian thistle (*Cirsium arvense* (L.) Scop.) in Tasmania. Weed Res. 15:77-81.

Best, K.F. 1975. The Biology of Canadian Weeds. 10. *Iva axillaris* Pursh. Can. J. Plant Sci. 55:293-301.

Blake, G.R. 1965. Bulk density. Pages 383 - 390 *in* C.A. Black, ed., Methods of Soil Analysis. Part I. American Society of Agronomy, Madison.

Bremner, J.M. and C.S. Mulvaney. 1982. Nitrogen - Total. Chap. 31, pages 595 - 624 *in* R.L. Page, R.H. Miller and D.R. Keney, eds., Methods of Soil Analysis II. Chemical and Microbiological Properties. 2nd ed., American Society of Agronomy, Soil Science Society Inc., Madison.

Buchholtz, K.P. 1962. Some Characteristics of Quackgrass and their Relation to Control. Proc. 16th North East Weed Control Conf. Pages 16-22.

Carson, A.G. 1974. Studies on competitive ability, seedling development, chemical control and translocation of dicamba and 2,4-D in Canada thistle. Ph. D. thesis. University of Guelph. 96 pp.

Chancellor, R.J. 1970. Biological background to the control of three perennial broad-leaved weeds. 10th Brit. Weed Control Conf. 3:1114-1120.

Charlton, W.A. 1965. Bud initiation in excised roots of *Linaria vulgaris*. Nature (London) 207:781-782.

Coukell, W.A. 1966. Carbohydrate levels in lateral roots of *Cirsium arvense* (L.) Scop. following various cultural and chemical treatments. M.Sc. thesis. University of Manitoba. 52 pp.

Cox, H.R. 1913. A battle with weeds. The Country Gentleman, February 8th, Curtis Publishing Co., page 26.

Detmers, F. 1927. Canada thistle, *Cirsium arvense* Tourn., Field Thistle, Creeping Thistle. Ohio Agric. Exp. Sta. Bull. no.414, 45 pp.

Donald, W.W. 1986. Stimulation of secondary shoot outgrowth from root buds of Canada thistle (*Cirsium arvense* (L.) Scop.) by soil drench application of chlorsulfuron. Abstr. Weed Sci. Soc. Am. 26:69.

Eliasson, L. 1961. the influence of growth substances on the formation of shoots from aspen roots. Physiol. Plantarum 14: 150-157.

Environment Canada. 1982. Canadian Climate Normals. Vol. 6. Frost. Canadian Climate Program, 275 pp.

Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. Forest Sci. 8:403-410.

Forsberg, D.E. 1962. Another look at the Canada thistle root system. Proc. 8th. Can. Soc. Agron., 94 pp.

Haderlie, L.C. and R.S. McAllister. 1981. Photosynthesis, assimilate translocation and root carbohydrates in Canada thistle. Proc. North Cent. Weed Control Conf. 36:160-162.

Hall, S.M. and J.R. Hillman. 1975. Correlative inhibition of lateral bud growth in *Phaseolus vulgaris* L. Timing of bud growth following decapitation. Planta 123:137-143.

Hamdoun, A.M. 1970. The effects of different levels of nitrogen upon *Cirsium arvense* (L.) Scop. plants grown from seeds and root fragments. Weed Res. 10: 121-125.

Hamdoun, A.M. 1972. Regenerative capacity of root fragments of *Cirsium arvense* (L.) Scop. Weed Res. 12:128-136.

Hauck, R.L. 1982. Nitrogen-Isotope ratio. Chap.36, pages 735 - 802 *in* R.L. Page, R.H. Miller and D.R. Keney, eds., Methods of Soil Analysis II. Chemical and Microbiological Properties. 2nd ed., American Society of Agronomy, Soil Science Society Inc., Madison.

Hauck, R.D. and J.M. Bremmer. 1976. Use of tracers for soil and fertilizer nitrogen research. Advances in Agronomy 28:219-266.

Hayden, A. 1934. Distribution and reproduction of Canada thistle in Iowa. Amer. J. Bot. 21:355-373.

Heide, O.M. 1968. Stimulation of adventitious bud formation in *Begonia* leaves by abscisic acid. Nature 219:960-961.

Hillman, J.R., V.B. Math and G.C. Medlow. 1977. Apical dominance and the levels of IAA in *Phaseolus* lateral buds. Planta 134: 191-193.

Hoagland, D.R. and D.I. Arnon. 1950. The water culture method for growing plants without soil. Calif. Agric. Expt. Sta. Circ. 347: 32 pp.

Hoefer, R.H. 1981. Canada thistle (*Cirsium arvense*) root bud initiation, biology, and translocation of carbon-14 labeled glyphosate as influenced by nitrogen, temperature, photoperiod and growth stage. Ph. D. thesis. University of Nebraska. 72 pp.

Hoefer, R.H. 1981. Growth and development of Canada thistle. Proc. North Cent. Weed Control Conf. 36:153-157.

Hodgson, J.M. 1958. Canada thistle (*Cirsium arvense* (L.)Scop.) control with cultivation, cropping and chemical sprays. Weeds 6:1-11.

Hodgson, J.M. 1968. The nature, ecology and control of Canada thistle. USDA Tech. Bull. 1386: 32 pp.

Hsiao, A.I. and G.I. McIntyre. 1984. Evidence of competition for water as a factor in the mechanism of root bud inhibition in milkweed (*Asclepias syriaca*). Can. J. Bot. 62:379-384.

Hunter, J.H. 1973. The biology of Canada thistle. Regional Extension Advisors Seminar, Brandon, Manitoba. 7 pp.

Hunter, J.H. 1985. A new way to control Canada thistle. Grainews, June. Pages 17-18.

Hunter, J.H. and L.W. Smith. 1972. Environment and herbicide effects on Canada thistle ecotypes. Weed Sci. 20:163-167.

Hunter, J.H. and G.I. McIntyre. 1974. Factors affecting the translocation of 2,4-D in leafy spurge. Weed Sci. 22:167-171.

Hunter, J.H., A.I. Hsiao and G.I. McIntyre. 1985. Some effects of humidity on the growth and development of *Cirsium arvense*. Bot. Gaz. 146:483-488.

Lauridson, T.C., R.G. Wilson and L.C. Haderlie. 1983. Effect of moisture stress on Canada thistle (*Cirsium arvense*) control. Weed Sci. 31:674-680.

Lin, C.S. and M.R. Binns. 1984. Working rules for determining the plot size and numbers of plots per block in field experiments. J. Agric. Sci., Cam. 103:11-15.

Maage, F. 1986. The effect of growth regulators on bud dormancy and winter injury in red rasberry. Act. Hort. 179:149-156.

Martin, A.R. 1971. Bud dormancy in Canada thistle as influenced by shoot excision and plant hormones. Diss. Abstr. Int. 32:3742.

Maxwell, B.D., M.E. Foley and P.K. Fay. 1987. The influence of glyphosate on bud dormancy in leafy spurge (*Euphorbia esula*) Weed Sci. 35:6-10.

McAllister, R.S. and L.C. Haderlie. 1981. Canada thistle root anatomy and root bud dormancy. Proc. North Cent. Weed Control Conf. 36:157-160.

McAllister, R.S. and L.C. Haderlie. 1985a. Seasonal variations in Canada thistle (*Cirsium arvense*) root bud growth and root carbohydrate reserves. Weed Sci. 33:44-49.

McAllister, R.S. and L.C. Haderlie. 1985b. Effects of photoperiod and temperature on root bud development and assimilate translocation in Canada thistle (*Cirsium arvense*). Weed Sci. 33:148-152.

McKeague, J.A. 1978. Manual of Soil Sampling and Methods of Analysis. 2nd ed., Canadian Society of Soil Science, 212 pp.

McIntyre, G.I. 1965. Some effects of the nitrogen supply on the growth and development of *Agropyron repens* (L.) Beauv. Weed Res. 5:1-12.

McIntyre, G.I. 1972. Developmental studies on *Euphorbia esula*. The influence of nitrogen supply on the correlative inhibition of root bud activity. Can. J. Bot. 50:949-956.

McIntyre, G.I. 1979. Developmental studies on *Euphorbia esula*. Evidence of competition for water as a factor in the mechanism of root bud inhibition. can J. Bot. 57:2572-2581.

McIntyre, G.I. and J.H. Hunter. 1975. Some effects of the nitrogen supply on growth and development of *Cirsium arvense*. Can J. Bot. 53:3012-3021.

Moore, R.J. 1975. The biology of Canadian weeds. 13. *Cirsium arvense* (L.) Scop. Can. J. Plant Sci. 55:1033-1048.

Nissen, S.J. and M.E. Foley. 1987. Correlative inhibition and dormancy in root buds of leafy spurge (*Euphorbia esula*). Weed Sci. 35:155-159.

Otzen, D. and A.H. Koridon. 1970. Seasonal fluctuations of organic food reserves in underground parts of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L. Acta Bot. Neerl. 19:495-502.

Parker, C. 1976. Effects on the dormancy of plant organs. Pages 165-190 *in* L.J. Audus ed., Herbicides, Physiology, Biochemistry, Ecology. Academic Press, New York.

Pavlychenko, T.K. 1943. Herbicidal action of chemicals on perennial weeds. Sci. Agric. 23:409-420.

Peterson, R.L. 1975. The initiation and development of root buds. Pages 125-161 *in* J.G. Torrey and D.T.Clarkson eds., The Development and Functions of Roots. Academic Press, London.

Peterson, R.L. 1979. Root buds in *Hieracium florentinum*: Effects of nitrogen and observations on bud outgrowth. Bot. Gaz. 140:407-413.

Phillips, I.D.J. 1975. Apical dominance. Annu. Rev. Plant Physiol. 26: 341-367.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley and Sons, New York, 385 pp.

Polowick, P.L. and M.V. Raju. 1982. The origin and development of root buds in *Asclepias syriaca*. Can.J. Bot. 60:2119-2125.

Regimbal, G.A. and A.R. Martin. 1985. Influence of growth regulators and nitrogen on leafy spurge (*Euphorbia esula*) control with picloram. Weed Sci. 33:109-113.

Robocker, W.C., R. Schirman and B.A. Zamora. 1972. Carbohydrate reserves in roots of Dalmatian toadflax. Weed Sci. 20:212-214.

Rogers, C.F. 1928. Canada thistle and Russian knapweed control. Colo. Agric. Exp. Sta. Bull. 348. 44 pp.

Rogers, C.F. 1929. Winter activity of the roots of perennial weeds. Science 69:299-300.

Russel, E.W. 1978. Soil Conditions and Plants. William Cloves and Sons Ltd, 10th Edition, London, 849 pp.

Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. USDA, Forest Service Gen. Tech. Rep. Int. 107. 12 pp.

Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. Ann. Rev. Ecol. Syst. 17:667-693.

Steel, G.D. and J.H. Torrie. 1980. Principles and Procedures of Statistics. A Biometrical Approach. 2nd ed., McGraw-Hill Book Co., New York, 633 pp.

Thind, K.B. 1975. the anatomy, physiology and biochemical factors controlling regeneration from roots of *Cirsium arvense* (L.) Scop., Ph.D. thesis, Brunel University, U.K., 234 pp.

Thomas, A.G. 1980. Relative abundance of Canada thistle on cultivated land in Canada. Canada thistle Symposium, Saskatoon, p. 1-15.

Wainwright, H., S.F. Todd and D.J. Price. 1986. Forcing and rooting dormant, single node cuttings of blackcurrant. Act. Hort. 183:331-338.

Welton, F.A., V.H. Morris and A.J. Hartzler. 1929. Organic food reserves in relation to the eradication of Canada thistle. Ohio Agr. Exp. Stat. Bull. no.441:1-25.

Werner, P.A. and R. Rioux. 1977. The Biology of Canadian Weeds. 24. *Agropyron repens* (L.)Beauv. Can. J. Plant Sci. 57:905-919.

Wilson, R.G. 1979. Germination and seedling development of Canada thistle (*Cirsium arvense*). Weed Sci. 27:146-151.

APPENDICES

APPENDIX 1

Nitrogen determination procedure for plants using the Kjeldahl analysis.

Digestion of Plants:

1. Add 3.5 g of $K_2SO_4/CuSO_4$ mixture to the digestion tube in which 0.04g to 0.05g of plant tissue is present.
2. Add one selenized boiling chip.
3. Add 10 ml of concentrated H_2SO_4.
4. Heat for 1.5 hour at 220°C.
5. Put condensers on digestion tubes, and heat at 360°C for 1 hour.
6. The nitrogen should now be in the form of NH_4^+.

Steam Distillation Procedure:

1. Digestion tube should be tightly connected to steam distillation head to allow steam into the tube.
2. Condensers are attached to the steam distillation head and the digestion tube.
3. 5 ml of 2% H_3BO_4 is placed underneath the condenser.
4. 30 ml of 50% (M/M) NaOH is slowly added to the digestion tube.
5. After the addition of an excess NaOH, collect 40 ml of distillate with H_3BO_4.
6. Clean the condenser using a digestion tube containing alcohol and place on the digestion head.
7. Determine nitrogen content by backtitrating with H_2SO_4.

8.

$$\text{Total N\%} = \frac{\text{Volume } H_2SO_4 * \text{Normality of } H_2SO_4 * \text{Molecular Weight of Nitrogen} * 100}{\text{Weight of sample}}$$

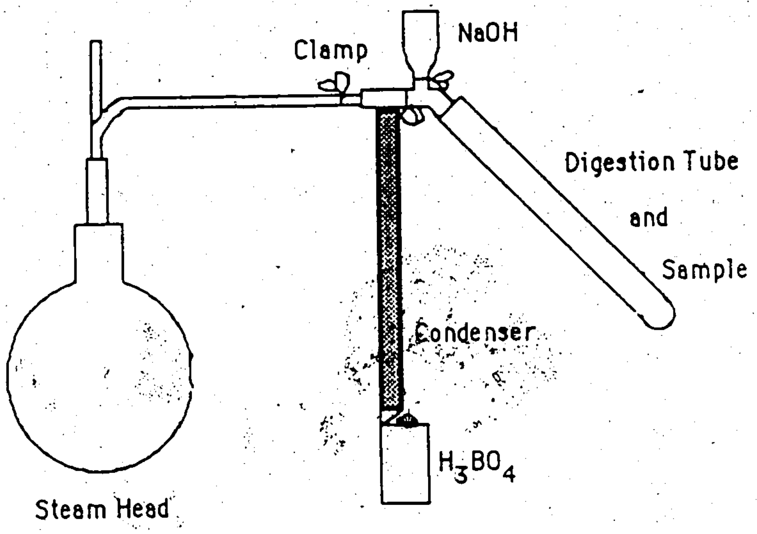


Figure 20. Setting of the steam distillation aparatus.

Preparation for the Mass Spectrometer:

1. Add an excess of H_2SO_4 to the sample of nitrogen.
2. Dry down the sample.
3. Form N_2 by adding NaOBr in the absence of air.
4. Put the gaseous nitrogen in the mass spectrometer.

APPENDIX 2

Soil acidity, potassium and extractable phosphate at the University of Alberta Ellerslie Research Station and the Edmonton Research Station sites in springs 1984, 1985 and 1986, and for the Navarre clay loam used in experiments 1 and 2.

2.1 Ellerslie Research Station

		June 3, 1984	
Depth	pH	PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.7	16.8	343
25-30	5.9	8.2	242
45-50	6.1	7.1	273
65-70	6.8	7.1	289

		June 9, 1985	
Depth	pH	PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.7	5.8	360
25-30	5.9	4.9	420
45-50	6.1	3.8	440
65-70	6.8	3.2	460

		May 17, 1986	
Depth	pH	PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.7	19.9	144
25-30	5.9	13.9	146
45-50	6.6	9.0	192
65-70	6.9	8.3	194

2.2 Edmonton Research Station

Depth	pH	June 3, 1984 PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.9	18.9	401
25-30	6.2	7.5	378
45-50	6.2	6.2	417
65-70	7.5	6.9	425

Depth	pH	June 9, 1985 PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.7	17.2	870
25-30	6.0	5.9	710
45-50	6.1	3.0	820
65-70	6.5	3.0	840

Depth	pH	May 10, 1986 PO_4	K
(cm)		(ppm)	(ppm)
5-10	5.8	30.8	434
25-30	6.3	14.7	321
45-50	6.3	6.9	339
65-70	6.5	5.8	439

2.3 Experiment 1

	Establishment					
	pH		PO_4		K	
Depth	Outdoors	Indoors	Outdoors	Indoors	Outdoors	Indoors
(cm)			(ppm)	(ppm)	(ppm)	(ppm)
5-10	6.0	5.9	40.1	55.8	370	437
25-30	6.0	5.9	40.1	55.8	370	437

2.4 Experiment 2

	June 9, 1985		
Depth	pH	PO_4	K
(cm)		(ppm)	(ppm)
5-10	6.0	25.1	860
25-30	6.0	25.1	860
45-50	6.0	25.1	860

	May 10, 1986		
Depth	pH	PO_4	K
(cm)		(ppm)	(ppm)
5-10	6.0	40.0	370
25-30	6.0	40.0	370
45-50	6.0	40.0	370

APPENDIX 3

Total soil nitrogen content at the University of Alberta Ellerslie Research Station and the Edmonton Research Station sites in 1985 and 1986 and for the Navarre clay loam used in experiments 1 and 2, at the beginning of experimentation.

3.1 Ellerslie Research Station

	1985 Total Soil Nitrogen						
	June 9	Aug 3		Sept 1		Sept 28	
Depth		-N	+N	-N	+N	-N	+N[a]
(cm)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
5-10	0.3	0.5	0.6	0.5	0.4	0.4	0.4
25-30	0.2	0.4	0.3	0.4	0.4	0.3	0.3
45-50	0.1	0.2	0.2	0.1	0.1	0.1	0.1
65-70	0.1	0.1	0.1	0.1	0.1	0.1	0.1

	1986 Total Soil Nitrogen							
	May 17		June 14		July 25		Aug 25	
Depth	-N	+N	-N	+N	-N	+N	-N	+N
(cm)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
5-10	0.5	0.5	0.4	0.5	0.5	0.5	0.4	0.5
25-30	0.4	0.4	0.3	0.1	0.3	0.3	0.1	0.3
45-50	0.2	0.1	0.2	0.3	0.1	0.2	0.1	0.1
65-70	0.2	0.1	0.1	0.2	0.1	0.2	0.1	0.1

	1987 Total Soil Nitrogen May 13	
Depth	-N	+N
(cm)	(%)	(%)
5-10	1.5	1.5
25-30	1.0	1.0
45-50	0.6	0.3
65-70	0.2	0.2

---

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

3.2 Edmonton Research Station

	1985 Total Soil Nitrogen June 9	
Depth	-N	+N
(cm)	(%)	(%)
5-10	0.4	0.5
25-30	0.3	0.3
45-50	0.1	0.1
65-70	0.1	0.1

	1986 Total Soil Nitrogen May 10	
Depth	-N	+N
(cm)	(%)	(%)
5-10	0.7	0.7
25-30	0.4	0.5
45-50	0.2	0.1
65-70	0.2	0.1

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

3.3 Experiment 1

Depth	Establishment Total soil Nitrogen Outdoors	 Indoors
(cm)	(%)	(%)
5-10	0.5	0.5
25-30	0.5	0.5

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

3.4 Experiment 2

Depth	Establishment Total Soil Nitrogen 1985	 1986
(cm)	(%)	(%)
5-10	0.6	0.5
25-30	0.6	0.5
45-50	0.6	0.5

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

APPENDIX 4

Soil inorganic nitrogen content at the University of Alberta Ellerslie Research Station and the Edmonton Research Station sites in 1984, 1985 and 1986 and for the Navarre clay loam used in experiments 1 and 2, at the beginning of the experimentation.

4.1 Ellerslie Research Station

Depth	1984 Soil Inorganic Nitrogen June 1
(cm)	(ppm)
5-10	10.6
25-30	5.6
45-50	4.3
65-70	4.3

1985 Soil Inorganic Nitrogen

Depth	June 9 -N	June 9 +N	Aug 3 -N	Aug 3 +N	Sept 1 -N	Sept 1 +N	Sept 28 -N	Sept 28 +N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	7.4	68.7	23.6	84.9	35.9	97.1	8.3	69.6
25-30	7.3	7.3	23.7	23.7	9.3	9.3	7.0	7.0
45-50	5.8	5.8	17.0	17.0	[illegible].1	6.1	8.0	8.0
65-70	5.5	5.5	5.0	5.0	5.1	5.1	5.0	5.0

1986 Soil Inorganic Nitrogen

Depth	May 17 -N	May 17 +N	July 25 -N	July 25 +N	Aug 25 -N	Aug 25 +N	Sept 18 -N	Sept 18 +N
(cm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	5.8	67.1	5.3	66.5	6.3	67.5	5.5	66.8
25-30	6.9	6.9	4.2	4.2	4.1	4.1	4.2	4.2
45-50	6.1	6.1	4.0	4.0	3.8	3.8	3.3	3.3
65-70	9.2	9.2	9.0	9.0	4.7	4.7	3.7	3.7

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied. The data were calculated by adding the soil inorganic nitrogen concentration of the untreated plots to the nitrogen concentration calculated from the rate of nitrogen applied in the top 10 cm and the soil bulk density.

4.2 Edmonton Research Station

Depth	1984 Soil Inorganic Nitrogen June 1 -N	 +N[a]
(cm)	(ppm)	(ppm)
5-10	20.8	58.9
25-30	10.2	10.2
45-50	7.9	7.9
65-70	7.5	7.5

Depth	1985 Soil Inorganic Nitrogen June 9 -N	 +N
(cm)	(ppm)	(ppm)
5-10	15.2	69.5
25-30	11.2	12.8
45-50	9.0	10.5
65-70	8.6	9.7

Depth	1986 Soil Inorganic Nitrogen May 10 -N	 +N
(cm)	(ppm)	(ppm)
5-10	8.4	62.7
25-30	11.6	7.7
45-50	10.0	10.8
66-70	9.0	9.3

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied. The data were calculated by adding the soil inorganic nitrogen concentration of the untreated plots to the nitrogen concentration calculated from the rate of nitrogen applied in the top 10 cm and the soil bulk density.

4.3 Experiment 1

Depth	Establishment Soil Inorganic Nitrogen Outdoors -N	Outdoors +N	Indoors -N	Indoors +N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	11.8	95.2	9.7	93.0
25-30	11.8	11.8	9.7	9.7

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied. The data were calculated by adding the soil inorganic nitrogen concentration of the untreated plots to the nitrogen concentration calculated from the rate of nitrogen applied in the top 10 cm and the soil bulk density.

4.4 Experiment 2

Depth	Establishment Soil Inorganic Nitrogen 1985 -N	1985 +N	1986 -N	1986 +N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	35.4	118.7	14.3	97.6
25-30	35.4	35.4	14.3	14.3
45-50	35.4	35.4	14.3	14.3

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied. The data were calculated by adding the soil inorganic nitrogen concentration of the untreated plots to the nitrogen concentration calculated from the rate of nitrogen applied in the top 10 cm and the soil bulk density.

APPENDIX 5

Soil inorganic nitrogen content at the University of Alberta Ellerslie Research Station and the Edmonton Research Station sites in 1985 and 1986 and for the Navarre clay loam used in experiments 1 and 2, at the end of the experimentation.

5.1 Ellerslie Research Station

1985
Soil Inorganic Nitrogen

	Aug 3		Sept 1		Sept 28	
Depth	-N	+N	-N	+N	-N	+N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	23.6	9.9	35.9	13.5	8.3	11.8
25-30	23.7	10.1	9.3	10.7	7.0	7.2
45-50	17.0	6.3	6.1	5.3	8.0	5.1
65-70	5.0	5.1	5.1	3.5	5.0	4.6

1986
Soil Inorganic Nitrogen

	May 10		July 25		Aug 25		Sept 18	
Depth	-N	+N	-N	+N	-N	+N	-N	+N
(cm)	(ppm	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	5.8	11.6	5.3	6.8	6.3	23.7	5.5	27.8
25-30	6.9	7.8	4.2	4.7	4.1	6.2	4.2	6.7
45-50	6.1	7.0	4.0	4.8	3.8	5.5	3.3	4.3
65-70	9.2	10.1	9.0	6.7	4.7	5.6	3.7	4.7

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

5.2 Edmonton Research Station

1985
Soil Inorganic Nitrogen
Aug 4

Depth	-N	+N[a]
(cm)	(ppm)	(ppm)
5-10	11.7	9.6
25-30	11.7	8.5
45-50	9.3	8.8
65-70	9.0	7.8

1986
Soil Inorganic Nitrogen
July 1

Depth	-N	+N
(cm)	(ppm)	(ppm)
5-10	10.6	8.1
25-30	5.4	6.5
45-50	10.1	6.4
66-70	7.4	6.5

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

5.3 Experiment 1

	Soil Inorganic Nitrogen			
	Outdoors		Indoors	
Depth	-N	+N	-N	+N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	9.1	41.9	6.1	25.4
25-30	17.5	17.1	6.7	5.7

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

5.4 Experiment 2

	Soil Inorganic Nitrogen			
	1985		1986	
Depth	-N	+N	-N	+N[a]
(cm)	(ppm)	(ppm)	(ppm)	(ppm)
5-10	44.3	44.9	12.2	25.4
25-30	25.8	35.7	16.0	22.9
45-50	27.3	35.0	14.8	23.1

[a] -N refers to plots on which no nitrogen was applied.
+N refers to plots on which 100 kg/ha nitrogen was applied.

APPENDIX 6

Average soil moisture tension at the University of Alberta Ellersie Research Station and the Edmonton Research Station sites in 1984, 1985 and 1986, and for the Navarre clay loam used in experiments 1 and 2 (see Appendix 7).

6.1 Ellerslie Research Station

	1984 Soil Moisture tension	
Depth	June 3	June 30
(cm)	(MPa)	(MPa)
5-10	0.15	0.13
25-30	0.25	0.43
45-50	0.74	0.90
65-70	0.65	0.60

		1985 Soil Moisture Tension		
Depth	June 9	Aug 3	Aug 23	Sept 28
(cm)	(MPa)	(MPa)	(MPa)	(MPa)
5-10	<1.50	0.06	0.48	0.18
25-30	<1.50	0.90	0.50	0.21
45-50	<1.50	<1.50	0.75	0.67
65-70	<1.50	<1.50	<1.00	0.90

			1986 Soil Moisture Tension		
Depth	May 17	June 14	July 25	Aug 25	Sept 20
(cm)	(MPa)	(MPa)	(MPa)	(MPa)	(MPa)
5-10	0.10	0.68	0.15	0.80	0.15
25-30	0.16	0.32	0.46	0.46	0.77
45-50	0.67	0.75	1.50	0.90	1.50
65-70	0.18	1.50	0.84	0.50	1.50

	1987 Soil Moisture Tension
Depth	May 13
(cm)	(MPa)
5-10	0.19
25-30	0.09
45-50	0.31
65-70	0.51

6.2 Edmonton Research Station

1984
Soil Moisture Tension

Depth	June 3	Sept 8
(cm)	(MPa)	(MPa)
5-10	0.13	0.08
25-30	0.16	1.50
45-50	0.52	0.72
65-70	0.47	0.70

1985
Soil Moisture Tension

Depth	May 15	June 30
(cm)	(MPa)	(MPa)
5-10	0.15	0.13
25-30	0.20	0.24
45-50	0.42	0.27
65-70	0.46	0.35

1986
Soil Moisture Tension

Depth	May 12	July 1
(cm)	(MPa)	(MPa)
5-10	0.13	0.23
25-30	0.10	0.27
45-50	>1.50	1.50
65-70	>1.50	0.45

6.3 Experiment 1

	Establishment Soil Moisture Tension	
Depth	Outdoors	Indoors
(cm)	(MPa)	(MPa)
5-10	0.15	1.5
25-30	0.15	1.5

	Harvest Soil Moisture Tension	
Depth	Outdoors	Indoors
(cm)	(MPa)	(MPa)
5-10	0.05	0.20
25-30	0.13	0.20

6.4 Experiment 2

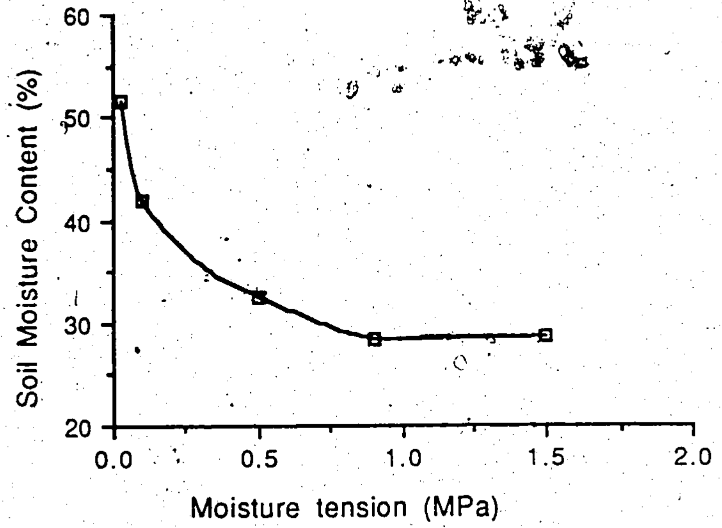
	Establishment Soil Moisture Tension	
Depth	1985	1986
(cm)	(MPa)	(MPa)
5-10	0.15	0.13
25-30	0.15	0.13
45-50	0.15	0.13

	Harvest Soil Moisture Tension	
Depth	1985	1986
(cm)	(MPa)	(MPa)
5-10	0.03	>1.50
25-30	0.03	>1.50
45-50	0.06	>1.50

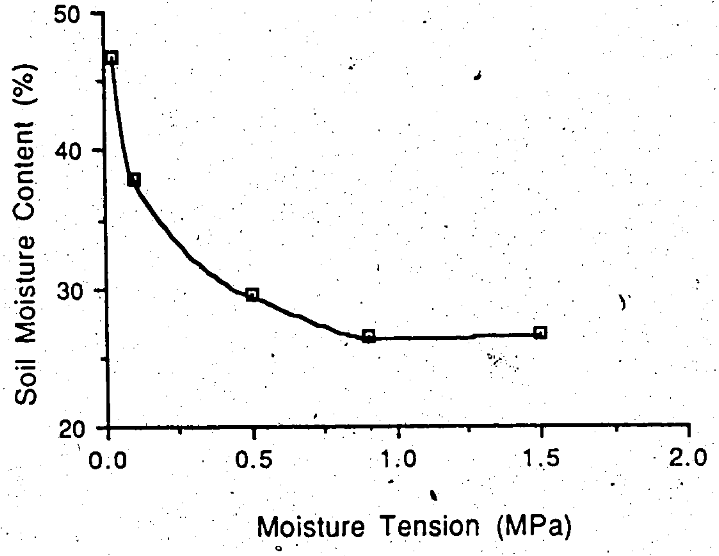
APPENDIX 7

Moisture retention curves used in calculating soil water potential in Appendix 6. (a) Edmonton Research Station site, 5 to 10 cm depth; (b) Edmonton Research Station site, 25 to 70 cm depth; (c) Ellerslie Research Station site, 5 to 10 cm depth; (d) Ellerslie Research Station site, 25 to 30 cm depth; (e) Ellerslie Research Station site, 45 to 70 cm depth. The soil moisture potential for Experiments 1 and 2 were calculated using (a).

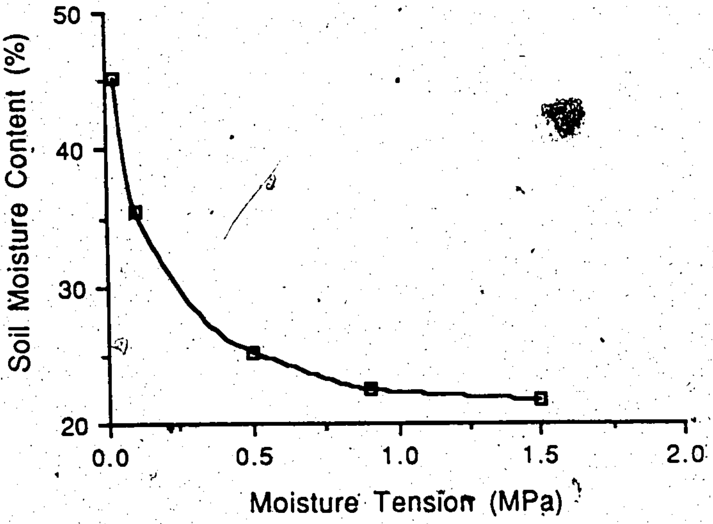
(a)



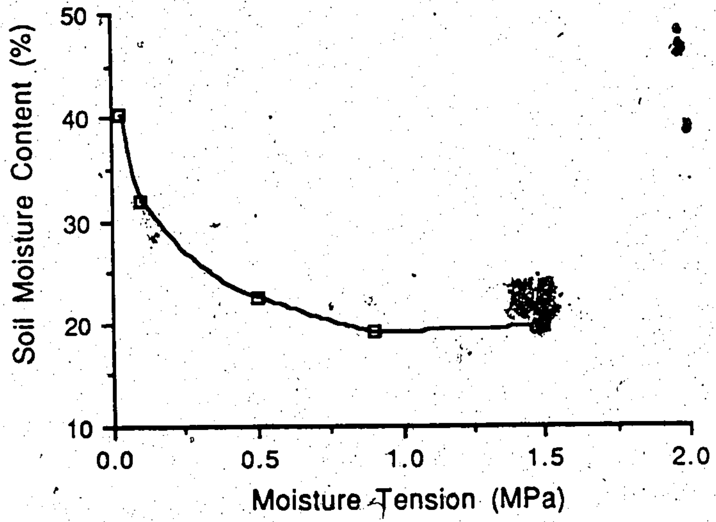
(b)



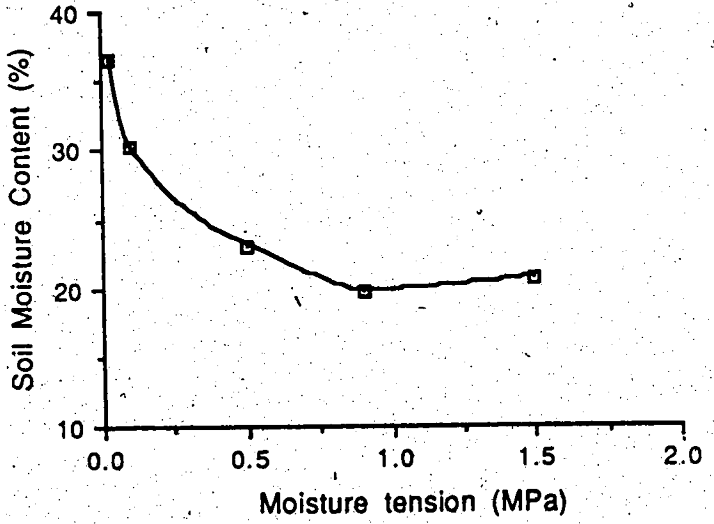
(c)


Soil Moisture Content (%)
50
40
30
20
0.0
0.5
1.0
1.5
2.0
Moisture Tension (MPa)

(d)


Soil Moisture Content (%)
50
40
30
20
10
0.0
0.5
1.0
1.5
2.0
Moisture Tension (MPa)

(e)


Soil Moisture Content (%)
40
30
20
10
0.0
0.5
1.0
1.5
2.0
Moisture tension (MPa)

APPENDIX 8

Average weekly minimum and maximum temperature and relative humidity and total weekly precipitation for the University of Alberta Ellerslie Research Station and the Edmonton Research Station for 1984, 1985 and 1986.

8.1 Ellerslie Research Station

			1984			
Week Starting		Precipitation	Temperature Max	Temperature Min	Relative Humidity Max	Relative Humidity Min
		(mm)	(°C)	(°C)	(%)	(%)
May	28	17	20	6	86	36
June	4	26	18	8	95	64
June	11	10	24	8	94	64
June	25	7	24	8	94	45
July	2	18	23	8	92	50
July	9	13	26	8	96	46
July	16	7	24	7	96	46
July	23	0	30	11	93	36
July	30	4	30	13	94	41
Aug	6	6	29	12	93	35
Aug	13	8	26	8	96	44
Aug	20	5	25	8	94	37
Aug	27	3	19	4	86	31
Sept	3	71	16	5	91	63
Sept	10	5	15	4	95	57
Sept	17	32	12	3	95	63
Sept	24	0	11	-3	93	46
Oct	1	0	21	4	89	35
Oct	8	6	18	6	85	43
Oct	15	6	1	-6	96	79

1985					
Weeks Starting	Precipitation	Temperature		Relative Humidity	
		Max	Min	Max	Min
	(mm)	(°C)	(°C)	(%)	(%)
May 27	6	18	4	89	38
June 24	1	22	7	84	39
July 1	0	30	10	86	23
July 8	9	29	9	89	38
July 15	3	28	10	88	37
July 22	4	26	8	89	30
July 29	4	31	11	89	28
Aug 3	15	24	7	89	40
Aug 12	3	22	7	88	49
Aug 19	7	22	8	87	51
Aug 26	3	21	5	89	41
Sep 2	4	14	2	89	55
Sept 9	2	18	6	88	57
Sept 16	10	12	2	89	59
Sept 23	7	11	3	88	51
Sept 3	1	15	-1	88	32
Oct 7	2	10	-3	82	44
Oct 14	1	10	-2	83	53
Oct 21	0	11	-3	79	29

1986					
Week Starting	Precipitation	Temperature		Relative Humidity	
		Max	Min	Max	Min
	(mm)	(°C)	(°C)	(%)	(%)
May 26	0	31	13	52	11
June 2	6	24	6	66	16
June 9	26	21	6	75	23
June 16	19	23	8	75	31
June 23	19	23	9	80	37
June 30	19	22	8	82	39
July 6	24	20	11	80	56
July 13	4	21	10	80	49
July 20	16	23	9	80	42
July 27	19	24	8	80	32
Aug 3	13	24	9	75	21
Aug 10	0	26	7	70	13
Aug 17	0	25	5	69	13
Aug 24	5	26	6	61	13
Aug 31	0	20	3	50	14
Sept 7	46	16	1	50	22
Sept 14	0	16	1	57	18
Sept 21	37	14	4	54	28
Sept 28	21	12	1	57	32
Oct 5	3	14	0	51	22
Oct 12	0	20	-1	51	15
Oct 19	0	19	-2	52	15
Oct 26	4	5	-5	50	29

8.2 Edmonton Research Station

Week Starting		Precipitation	Temperature Max	Temperature Min	Relative Humidity Max	Relative Humidity Min
1984						
		(mm)	(°C)	(°C)	(%)	(%)
May	28	20	16	7	94	43
June	4	30	18	8	98	64
June	11	11	26	9	99	45
June	18	3	23	5	96	45
June	25	17	27	11	99	44
July	2	18	23	8	96	47
July	9	6	27	11	98	43
July	16	0	26	9	97	56
July	23	6	32	12	91	49
July	30	7	33	14	98	56
Aug	6	6	32	13	94	54
Aug	13	10	24	14	94	40
Aug	20	5	20	14	70	35
Aug	27	5	21	4	89	30

1985					
Week Starting	Precipitation	Temperature		Relative Humidity	
		Max	Min	Max	Min
	(mm)	(°C)	(°C)	(%)	(%)
May 27	5	20	6	99	70
June 3	3	19	5	93	49
June 10	5	17	5	95	54
June 17	9	19	6	87	52
June 24	10	16	6	91	56
July 1	5	26	11	91	56
July 8	4	26	11	94	55
July 15	2	22	7	98	58
July 22	0	23	9	98	58
July 29	13	26	9	99	56
Aug 5	12	22	8	99	60
Aug 12	0	22	7	98	69
Aug 26	0	23	6	95	50
Sept 2	8	18	5	91	63
Sept 9	3	11	3	89	60
Sept 16	9	-	-	88	57

	1986				
Week Starting	Precipitation	Temperature		Relative Humidity	
		Max	Min	Max	Min
	(mm)	(°C)	(°C)	(%)	(%)
May 26	0	32	13	81	44
June 2	3	25	7	88	47
June 9	21	22	6	89	46
June 16	20	25	7	89	49
June 23	10	24	9	92	49
June 30	18	23	8	93	54
July 6	32	20	9	93	65
July 13	86	24	10	97	67
July 20	9	26	10	99	57
July 27	17	26	9	99	53
Aug 3	0	26	9	96	51
Aug 10	0	27	8	94	45
Aug 17	1	27	7	95	45
Aug 24	0	29	7	98	49

APPENDIX 9

Soil bulk densities at the University of Alberta Ellerslie Research Station site and Edmonton Research Station site as well as the bulk density of the the Navarre clay loam used in experiments 1 and 2. The paraffin clod method used is described by Blake (1961).

Depth	Ellerslie Research Station	Edmonton Research Station
(cm)	(g/cm^3)	(g/cm^3)
5-10	1.63	1.84
25-30	1.88	1.92
45-50	2.09	2.05
65-70	2.06	2.05

Navarre Clay Loam
1.20 g/cm^3