UNIVERSITY OF ALBERTA

GROWTH RESPONSE OF
CALAMAGROSTIS CANADENSIS
IN RELATION TO
VARIABLE LIGHT AND NUTRIENT LEVELS
AND IN RELATION TO
RHIZOME SEVERING

©

BY

R. ALLAN POWELSON

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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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 Growth Response of Calamagrostis canadensis In Relation To Variable Light and Nutrient Levels and In Relation to Rhizome Severing submitted by R. Allan Powelson in partial fulfilment of the requirements for the degree of Master of Science.

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Date: November 30, 1989

ABSTRACT

The pattern of biomass allocation employed by Calamagrostis canadensis under different light and nutrient regimes was studied. The major findings of a greenhouse experiment testing the relationship between light and nutrient level and biomass allocation in C. canadensis are as follows: plant growth, including rhizome production, increases with light intensity and nutrient availability; nutrient availability only alters plant growth when light intensity is at moderate and high levels; numbers of rhizomes produced and proportional biomass allocation to rhizomes reaches a peak under moderate light intensities but the allocation of total biomass to these rhizomes is lower than under high light intensities; population alters the amount of biomass produced but has no affect on the proportional allocation of biomass within the plant. Under field conditions tiller weight, rhizome weight, rhizome diameter and non-structural carbohydrate content of rhizomes increased as canopy crown closure decreased. Proportional allocation of biomass to rhizomes, however, reached a maximum under an open canopy.

In a second study, the dimensional and carbohydrate characteristics of C. canadensis rhizome segments adjacent to the parental base and rhizome apex were recorded and compared. Rhizome segments adjacent to the apex were found to be thicker, heavier, and have a higher non-structural carbohydrate content than rhizome segments adjacent to the parental base. Nodal length in both types of rhizome segments increased with distance from either the parental base or rhizome apex. Also in this study, the frequency of bud development in relation to the number of dormant buds on the rhizome segment and bud position on the rhizome segment was recorded. Findings from this study were as follows: rhizomes buds adjacent to the rhizome apex have a higher regenerative capacity than buds adjacent to the parental base; A priority of bud development which favours the bud closest to the parental base was established when the parent was excised; No priority of bud development arose on rhizome segments adjacent to the apex. It was also determined that tiller and rhizome production from developed buds was more affected by the condition of the environment it emerged into than the condition of the originating rhizome.

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INTRODUCTION

In the boreal forest, marsh reed grass (Calamagrostis canadensis (Michx) Beauv.) is wide spread and dominates early successional sites. This species often disrupts reforestation efforts by severly hampering the establishment of conifer seedlings. Norokorpi (1986) found that white spruce (Picea glauca (Moench) Voss) seedling growth rates were slow and mortality was high in sites with thick sods of C. canadensis. The poor regeneration of conifers on these sites has been related to root competition between the young seedlings and the grass (Sims and Mueller-Dombois, 1968). The thick canopy produced by C. canadensis can also cause significant shading of conifer seedlings (Eis, 1981). The high amounts of litter produced by the above ground portion of the grass can smother seedlings when compressed by snow (Arlidge, 1967; Blackmore and Corns, 1979; Eis, 1981). Also, conifer seeds falling into this litter may be suspended above the soil and the germinants desiccate as the litter layer dries in the spring (Haeussler and Coates, 1986). The thick layer of organic mulch will delay soil heating in the spring (Haeussler and Coates, 1986) which can reduce conifer seedling root development and growth (Konowalyk, 1989).

Marsh reed grass is a perennial, tussock-forming grass with many creeping rhizomes (Polunin, 1959; Watson et al., 1980; Sims et al., 1984; Haeussler and Coates, 1986). However, when grown under optimum field conditions it forms continuous sods with the potential to occupy all available growing sites (Eis, 1981).

Marsh reed grass stems have slightly drooping leaves and are usually between 60 to 120 cm tall (Haeussler and Coates, 1986), although, plants 1.5 m tall have been observed on British Columbia cutblocks (Eis, 1981). C. canadensis also, produces a very fine root system which provides a large absorbing surface for the uptake of water and nutrients from the soil (Younkin, 1973). Only 30 to 35% of the total biomass production, however, is in the root system suggesting a slightly different priority in the use of photosynthates, as compared to commercial grass species which allocate more biomass to below ground organs (Younkin, 1973).

Phenology studies from southern Alaska indicated that marsh reed grass completes its height growth by mid - July and is fully headed by mid - August (Mitchell and Evans, 1966; Mitchell, 1974). Inflorescences vary from a dense to an open drooping panicle (Haeussler and Coates, 1986). Calamagrostis canadensis also portrays agamospermy (Kigel and Koller, 1985) (i.e. seed containing an embryo that has arisen without meiosis and fertilization of the female gamete). It is also non-pseudogamus, thus it does not need the fertilization of other flowers on the same plant to bring about agamospermy (Kigel and Koller, 1985).

Whether by fertilization through wind pollination or through asexual means, marsh reed grass produces a relatively small but highly viable seed (Hitchcock, 1971). Achenes are small, light and covered by a fine hair. Seed is produced annually provided that environmental conditions are favourable (Younkin, 1974). Thus, in tundra communities marsh reed grass rarely produces flower heads (Hernandez, 1973).

Younkin (1974) reported that seed yield of C. canadensis is low.

Observations of marsh reed grass stands in northern Alberta, however, have shown high seed yields. The seed has also been reported to have no appreciable dormancy and Younkin (1974) reported a 90% germination rate without cold stratification (Conn and Farris, 1987). Sims et al. (1984) reported that it should take 8 days at 20^{o} C. to germinate at the rate reported by Younkin (1974). However, when the seed has has been stored at $-18^{o}C$ for approxiametly 6 months it requires a period of wet stratification for seven days at 5^{o} C. (Powelson, unpublished) to be able to germinate and achieve the high rates of germination stated by Younkin (1974).

The wind dispersed seed of C. canadensis is able to germinate under a range of moisture and temperature regimes (Younkin, 1973). However, Younkin (1974) reported that once the seed germinates it establishes poorly and may not reach maturity due to its low survival rate under natural conditions (Younkin, 1973). The reasons for low survival, however, were not discussed.

Marsh reed grass consists of three chromosome races, the tetraploid (2n=28), hexaploid, and the rare octaploid genotypes (Mitchell, 1968), with the hexaploid and octaploid races occuring in Canada (Mitchell, 1974). The phenology expressed by these three chromosome races differs only slightly, thus their distinction into different subspecies is unneccessary (Mitchell, 1968). This suggests that the results of studies done on one race can be applied with confidence to the other races.

Marsh reed grass is commonly found at mid-elevation of cool to cold regions of the northern hemisphere and is widely distributed in

North America (Younkin, 1973; Laughlin et al., 1984). It has a wide ecological amplitude, occurring in lowland wet areas to wind-swept alpine ridges (Hanson, 1951; Mitchell, 1968; Younkin, 1973; Norton et al, 1987). It can withstand exposed conditions, its roots are tolerant of low soil temperatures, and it is extremely winter hardy (Klebesadel, 1965; Younkin, 1974; Mitchell, 1978; Watson et al, 1980; and Laughlin et al, 1984). Marsh reed grass has been found to be abundant on moist, high elevation sites (Corns and LaRoi, 1976), on upland mesic sites (Hernandez, 1973), and on both organic and inorganic soils (Watson et al, 1980). It is also adapted to a wide range of soil textures (Watson et al, 1980). Sods have been reported to be as thin as 1 - 2 cm on poor sandy soils and as thick as 4 - 8 cm on loamy sand soils (Sims and Mueller - Dombois, 1968). Marsh reed grass can also survive soil moisture regimes ranging from imperfectly to moderatly well drained (Watson et al, 1980). It is characteristicly found on moist sites with fine-soils that have good water holding capacities, or on sandy soils with high water tables (Polunin, 1959; Mueller-Dombois and Sims, 1966), and is tolerant of flooding (Watson et al, 1980). Marsh reed grass will not germinate under drought conditions, although, once established it has very good drought resistance (Mueller-Dombois and Sims, 1966).

While only moderately tolerant of saline soils, marsh reed grass can survive soil pH values as low as 3.5 (Mitchell, 1978; Watson et al, 1980; Laughlin et al, 1984). C. canadensis is considered to possess moderate nutritional requirements (Haeussler and Coates, 1986). Additions of nitrogen, phosphorus, and potassium, however, have been shown to stimulate flowering rates and increase vegetative growth (Mitchell and Evans, 1966; Watson et al, 1980).

Marsh reed grass is characteristic of, but not restricted to, disturbed early successional open habitat (Younkin, 1973; Conn et al, 1984). In northern Alberta it is mainly found in the openings of moist forested sites and along streambanks (Blackmore and Corns, 1979 and Eis, 1981). Ground cover by marsh reed grass under a mature forest canopy, however, is much lower than in adjacent forest openings or clear cuts (Corns and LaRoi, 1976). Marsh reed grass prefers the open sites but will tolerate the partial shade of a mature forest canopy where it grows in a vegetative state (Watson et al, 1980).

Under a forest canopy and on undisturbed sites the growth rate, height and seed production of the marsh reed grass is greatly reduced; only 5% of shoots produce seed (Younkin, 1973). After canopy removal either by logging (Eis, 1981) or after a light burn, biomass production of marsh reed grass exhibited a sharp upward trend (Dyrness and Norum, 1983). The surviving rhizomes and plants expanded quickly and dominated the site under the new growing conditions (Ahlgren, 1960; Wein and Bliss, 1973; Younkin, 1973; Frisque et al, 1978).

Disturbance of the soil facilitates a greater rate of invasion by marsh reed grass (Haeussler and Coates, 1986). Eis (1981) found that it heavily invaded the moist to wet compacted soils on roads, landings and skid trails of harvested sites. Aldridge (1967) found that 2 to 3 years after scarification marsh reed grass was a serious competitor of mounded sites within wet depressional areas. Heavy cultivation can control established plants (Haeussler and Coates, 1986). Areas of newly exsposed soil, however, are rapidly invaded by adjacent, undisturbed plants through rhizome extension (Haeussler and Coates, 1986).

When compared to commercial grass species marsh reed grass establishes slowly, although, by the end of the third growing season its cover and biomass production can exceed or equal commercial species grown under similar conditions (Watson et al, 1980). Marsh reed grass shows a higher stem density on less productive sites than on more productive sites (Mueller-Dombois and Sims, 1966), and once a marsh reed grass stand is well established it can survive, possibly, for one hundred years or more (Watson et al. 1980). The portion of marsh reed grass which is above ground dies back at the end of each growing season. This produces a thick organic mulch, that may constitute 50% of the total ground cover after a few year's growth on a site (Sylvester and Wein, 1981).

Declines in yield of up to 20% have been shown to occur when this grass was cut 2 to 4 times during the growing season (Mitchell and Evans, 1966). Herbicides applied during the growing season can provide good to excellent control of marsh reed grass. Glyphosate applied as a foliar spray and hexazinone applied as a liquid spray provide good to excellent control depending on the rate and timing of application (Blackmore and Corns, 1979; Expert Committee on Weeds, 1984 cited by Haussler and Coates, 1986).

General Plant Responses to Light:

The supply of light to an individual plant is determined by day length, season, canopy structure, crown closure, cloud cover and many other factors related to the general environment (Spedding, 1971). Once germination has been achieved, further development is also subject to control by the light environment (Salisbury and Ross, 1985). Plant morphology is substantially modified by its light environment (Vince-Prue and Canham, 1983). With many species increased growth, or biomass accumulation, is associated with increased light intensities (Evans et al, 1964), until saturation of photosynthesis occurs. In C_3 grasses light saturation of the photosynthetic system occurs at about 25% of full sunlight (Redmann and Reekie, 1982).

Full exploitation of light requires a more complex receiving surface than a single horizontal layer of leaves (Spedding, 1971). A major aspect of the attenuation of light within a grass sward is the amount of leaf displayed (Spedding, 1971). Theoretically in order to attain maximum production, a plant would display as many leaves as possible, within a unit ground area, to incomming radiation (Mooney, 1972). Spreading of the light over a larger leaf area decreases the average light intensity intercepted by each individual leaf, resulting in more efficient energy conversion (Redmann and Reekie, 1982). The increase in leaf area at low light intensities may partly compensate for the reduced net photosynthesis per leaf (Williams, 1980).

The long slender leaves of grasses, many of which are held relatively erect, favour the penetration of light well into the sward.

This results in active photosynthesis by the lower leaves (Evans et al, 1964), which tend to supply the roots and developing tillers with photosynthate (Redmann and Reekie, 1982). Environmental condition has little effect on the initiation of tillers, but development of the tiller bud past this early stage is highly dependent on the condition of the environment (Evans et al, 1964; Kigel and Koller, 1985). When environmental conditions inhibit or retard plant growth, the tiller bud either does not develop further, or begins development only to die before the tiller appears (Evans et al, 1964).

Tillering is controlled in part by the phytochrome system (Salisbury and Ross, 1985) and is retarded when the light transmitted to the stem bases is rich in far-red light and promoted by light rich in red wavelengths (Salisbury and Ross, 1985). In several species high light intensity is associated with high tillering, while low light intensity, which is associated with low carbohydrate status, usually results in low tillering rates (Evans et al, 1964; Laude, 1972; Williams, 1980).

Low light intensities promote leaf development at the expense of root development (Anderson et al. 1969), while high light intensities promote root growth (Evans et al. 1964). Plants grown in shade tend to adjust their root to shoot ratio in favour of shoots, which results in a feeble root system and a lowered soil volume to be explored during periods of water and nutrient shortage (Mooney, 1972; Grime, 1977; Lovett-Doust, 1987).

After grasses flower in the summer there is often a decline in leaf growth, some renewal of tillering and root growth and in rhizomatous species rapid development of rhizomes (Evans et al. 1964). Rhizome production often reaches a peak in late summer (Evans et al. 1964), suggesting that photoperiod may play an important role in their production. Light intensity also impacts the production and development of rhizomes. High light intensity has been indicated as necessary for new primary rhizome growth (Palmer, 1958), while a decrease in the daily input of light energy reduced the relative allocation of biomass to rhizome growth (Kigel and Koller, 1985). At low plant densities, thus high light penetration into the sward, increased allocation to clonal growth facilitates rapid local spread with low risk (Bazzaz and Reekie, 1985).

General Responses of Plants to Nutrients:

Nutrient supply must be maintained at an adequate level for normal tillering (Evans et al., 1964; Laude, 1972; Willaims, 1980) and any increase in nutrient supply will increase tiller production. The high production rate of tillers stimulated by fertilization may cause the density stress that shortens the life expectation of older tillers (Noble et al., 1979). Laude (1972) found that nitrogen fertilization only stimulated tillering if the light intensity was above 422 ft. candles.

Nitrogen fertilization has been reported to reduce rhizome growth and promote the emergence of tillers (Kigel and Koller, 1985) in *Agropyron repens* (L.) Beauv., *Poa spp.*, and *Bromus inermis* Leyss. (Evans et al., 1964). Lovett - Doust (1987) found that in *Ranunculus repens* L. a high nutient supply increased allocation to leaves on daughter ramets and to stolons. From this finding it was stated that a greater supply of nutrients clearly allows more growth, and in clonal species this manifests itself as more clonal growth (Lovett-Doust, 1987). Lovett-Doust (1987) also found that when resources are restricted, there is proportionately less emphasis on growth of ramets, such that lower resources allow less growth and relatively less production in the daughter ramets (Lovett-Doust, 1987). Also, it has been demonstrated in Rubus hispidus L. that the switch from asexual growth to sexual reproduction results from nutrient depletion (Abrahamson, 1975).

In order to survive in a habitat where resources are distributed in patches, a clonal plant may have to continually search for and exploit new patches of resources (Cook, 1983; Loehle, 1987). The capacity to detect gradients of nutrients, then initiate adventitious roots and establish shoots may greatly increase the success of the clone (Cook, 1983; Loehle, 1987). Stolons are capable of detecting gradations of nutrients in the soil and then establishing ramets in locations of higher nutrients (Cook, 1983). Loehle (1987) stated that runners (rhizomes) can change direction of growth to take advantage of microsite differences, put down more roots at more fertile locations and terminate elongation at sites which are more beneficial for growth. The regulation of ramets actually represents the regulation of movement of the biomass of the clone in space, controlled by a number of developmental processes (Cook, 1983) which could be regulated by environmental conditions. Linear clonal growth, especially in nutrient poor habitats, may be related to the efficient capture of nutrients by the roots of extending rhizomes and their efficient transport to other parts of the clone (Noble and Marshall, 1983). The reverse situation may, however, also apply in that persistence of the rhizome allows nutrients to be recycled from the older phases of development to the juvenile phase of growth at the leading edge of the clone (Noble and Marshall, 1983). Either way, nutrient deficiencies would tend to promote rhizome growth. Fitness may depend more on maximizing the lateral exploitation of the soil and its nutrient resource than on vertical growth and light capture (Noble et al., 1979).

Grass roots generally branch freely and form a fibrous system (Barnard, 1964). Branching patterns of roots are more flexible than those of shoots, perhaps because soil environments vary more than those of the air (Salisbury and Ross, 1985). Even though root morphology is genetically controlled, soil environments influence the final rooting pattern (Salisbury and Ross, 1985). There is good evidence that at a plant organ level, the carbon costs of resource uptake varies with the availability of the resource (Bazzaz and Reekie, 1985). It follows that a plant would have to allocate more and more carbon to root growth to extract the same amount of water and nutrients as these resources became more scarce (Mooney, 1972; van Andel, 1975; Grime, 1977; Bazzaz and Reekie, 1985; Lovett-Doust, 1987).

Rhizomes and Vegetative Reproduction:

When population density and competitive interactions are high or habitat instability increases, plants should put a greater proportion of their resources into seed production (Abrahamson, 1975).

Conversely, in a stable, predictable habitat with low population densities and where clonal expansion is possible, vegetative reproduction should be favoured (Abrahamson, 1975). However, Barkham (1980a) stated that environmental stress can bring about a high rate of vegetative reproduction. Thus, early successional plants have a greater reproductive effort than later successional species (Newell and Tamer, 1978). Vegetative reproduction may be favoured as a persistence strategy, because vegetative reproduction requires relatively little nutrient investment per successful offspring (Loehle, 1987). It is the outcome of vegetative growth which produces relatively fast, low risk local spread as the growth of the clone continues (Abrahamson, 1975).

A plants' ability to protect the original germplasm contributes to their indefinite regeneration and reproduction (Kigel and Koller, 1985). Organs and structures of vegetative reproduction are able to depend on supply of nutrients and water from the parent plant for a long period (Kigel and Koller, 1985). Parent plants may also store assimilates in perennating strutures (rhizomes) for subsequent utilization by activated buds (Kigel and Koller, 1985).

New individual plants arise asexually when buds (axillary, apical or adventitious) grow into autonomous, adventitiously rooted tiller groups, which at some point become separated from each other (Kigel and Koller, 1985). For rhizomatous and stoloniferous grasses, in which groups of tillers are separated along more or less horizontal stems, new tiller groups are subsidized by carbon imported from older groups (Hutching and Bradbury, 1986). Independence is attained quickly, however, and only severe impairment of photosynthetic capacity or depletion of carbohydrates in a tiller group will stimulate renewed carbon translocation from the older groups of tillers (Hutchings and Bradbury, 1986).

Rhizomes are produced when intercallary activity occurs independently of inflorescence formation (Barnard, 1964). Rhizomes differ from primary shoots in their origin from pre-existing shoots rather than from the embryo (Gould and Shaw, 1983) and in their horizontal rather than vertical orientation. Rhizomes are recognizable as stems by the regular node and internode spacing and by the production of scale leaves, shoot buds and adventitious roots at the nodes (Gould and Shaw, 1983).

Although rhizomes are reproductive structures of the plant, it should also be noted that these structures must serve as carbohydrate storage organs in order to carry the dormant rhizome buds over some stress period, such as winter cold or summer drought (Berg, 1972; Luthra et al., 1985). In perennial plants surplus carbon may be stored and then utilized during periods when there are high construction demands (Mooney, 1972). Seasonal changes in carbohydrate levels in grass plants suggest that regrowth following winter or drought is dependent on carbohydrates stored in rhizomes (Berg, 1972; White, 1973; Redmann and Reekie, 1982). Rhizomes are extremely rich in stored food (mostly carbohydrates) (Kigel and Koller, 1985), and are frequently the major source of reserve carbohydrates (Whitney, 1982). Starch and various mono - and disaccharides are the primary storage products of plants, however, fructosans (polysaccharides with fructose repeating units) are common storage products of cool temperate grasses (Mooney, 1972; Smith, 1972; White, 1973).

As with seeds, food storage in rhizomes is usually associated with bud and root dormancy of the perennating units (Kigel and Koller, 1985). The accumulation of dormant buds on rhizomes forms a "bank" equivalent in many ways to a seed "bank", that confers on the plant an ability to regenerate after damage (Noble et al., 1979). The greater content of stored food in rhizomes allows the new sprouts a faster shoot growth and more rapid emergence with greater mechanical resistance as compared to seedlings (Kigel and Koller, 1985).

Long rhizomes serve as a means of vegetative propagation when they become severed by natural or artificial means (Barnard, 1964). Without severence of the rooted nodes the individuals may extend over large areas and become a system of practically independent units (Barnard, 1964). If disconnected from the parent plant, these units may have the capacity of independent existence for prolonged periods in an inactive (dormant) state under harsh environmental conditions (Kigel and Koller, 1985). While in this form they can be widely dispersed by exogenous agents (Kigel and Koller, 1985). The dispersal of vegetative propagules is partially controlled by exogenous factors that disturb their soil habitat and at the same time, detach them from their parents (Kigel and Koller, 1985). Epilobium adenocaulon Hausskw and Epilobium montanum L. are not well adapted to vegetative spread, however, the overwintering buds and rossettes are easily detached from the remains of the parent plant by burrowing animals or horticultural practices which can cause them to be widely spread (Myerscough and

Whitehead, 1966). In perrenial agricultural weeds, such as Agropyron repens, the most prevalent factor which contributes to their persistence and spread is cultivation (Kigel and Koller, 1985). The large amounts of readily available carbohydrates stored in rhizomes and buds on the rhizome allows quackgrass to withstand treatments that control other weeds (Majek et al., 1984).

In lightly burned areas, the great majority of early postburn plants appear as a result of sprouting of underground parts (rhizomes) (Dyrness and Norum, 1983). Some propagules exhibit inhibition of their bud activation after they have been disconnected from their parent, however, on others, growth of the propagule may be promoted by the disconnection from the parent plant (Kigel and Koller, 1985). The potential for regeneration in rhizome buds is determined by different factors, with the upper limit of developed buds upper limit depending on the number of nodes per unit length or segment length (Kigel and Koller, 1985).

The behaviour of rhizomes can be strongly influenced by both hormones produced by the parent plant and nutritional factors (Cook, 1983). Agropyron repens spreads by means of rhizomes that exhibit a typical apical dominance. Detachment of the rhizome from the parent plant may activate or inhibit the axillary buds on the rhizome, while decapitation of the apical bud activates the most distal axillary bud (Goodin, 1972; Kigel and Koller, 1985). Dormancy of axillary buds is controlled by endogenous growth regulators originating from both the apical bud and the parent plant (Kigel and Koller, 1985). Inactivity of the buds may be due to inherent dormancy. Buds may be released from dormancy either by environmental signals or through internal changes (Kigel and Koller, 1985). The tendency of rhizome buds to develop into leafy shoots was ascribed to a reduced supply of assimilates from the parent shoot growing at low light intensities and high temperatures (McIntyre, 1970; Kigel and Koller, 1985). In addition, the transition may take place as a result of a transformation of the tropic response of apices of rhizomes to negative geotropism, which results in the emergence of the apical bud from the soil to produce an erect shoot (Kigel and Koller, 1985). Such transformations may take place while the shoot apex is still within the soil, but rhizomes disturbed through cultivation may promote this transformation, either by exposing the apex to light or by morphogenetic changes brought about by the disconnection from the parent plant (Kigel and Koller, 1985).

After fragmentation and activation of the axillary buds, the fastest growing bud assumes dominance over the rest of the buds and inhibits any further expansion by them (McIntyre, 1969; McIntyre, 1970; McIntyre, 1971; McIntyre, 1972; Chancellor, 1974; Leakey et al. 1977b; Leakey et al, 1978a; Leakey et al., 1978b; Kigel and Koller, 1985). If this new dominant bud is removed or destroyed in some manner or further fragmentation occurs, the inhibited buds will resume their growth (Leakey et al., 1977b; Leakey et al, 1978a; Leakey et al., 1978b; Kigel and Koller, 1985). When light was applied after the buds of Poa pratensis L. had sprouted in darkness, it prevented the onset of dominance, and all buds grew equally (Nyahoza et al., 1974; Kigel and Koller, 1985). The rhizome apex exerted a dominating influence on shoot growth of axillary buds in Sorghum halepense [L.] Pers.

(Beasely, 1970). If the rhizome apexes of A. repens and S. halepense were not removed, axillary bud growth was non - existent or significantly less than that from decapitated rhizome pieces (McIntyre, 1969; Beasely, 1970; McIntyre, 1970; McIntyre, 1971; McIntyre, 1972; Leakey et al., 1977b; Leakey et al, 1978a; Leakey et al., 1978b). With removal of the apex, buds closest to the apex had greater shoot extension than positions further away (Beasely, 1970).

Seasonality of growth from fragments of rhizomes commonly occurs in many creeping perrennials (Palmer, 1958; Leakey et al., 1977a). Regenerative capacity of Agropyron repens rhizomes is at a maximum in April (Leakey et al., 1977a). Leakey et al. (1977b) stated that this seasonal pattern of regenerative capacity is due to the seasonal variation of stored nitrogen and dry weight. Also, the amount of carbohydrates stored in the rhizome varies with season (Berg, 1972; White, 1973; Redmann and Reekie, 1982), which may have an impact on regenerative capacity.

After reviewing the literature of Calamagrostis canadensis there are several factors that need more study: 1) What are the impacts of different light and nutrient levels on the pattern of biomass allocation in marsh reed grass? and 2) What are the growth responses of dormant rhizome buds severed from the parent plant and rhizome apex when grown under full light conditions?

The results generated from these studies provide a basic understanding of the growth response of the marsh reed grass on disturbed sites. This may provide the basis for management of C. canadensis and lower its impact on coniferous regeneration.

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Light and Nutrient Effects on Biomass Allocation of Calamagrostis canadensis:

During the successional sequence of a boreal forest site, the understory environment undergoes dramatic shifts in light intensity and nutrient availability (Grime, 1977; Scheiner and Teeri, 1986; Kimmins, 1987). The removal of the overstory through fire or forest harvesting causes a large increase in light intensity and nutrient availabilty upon the site (Kimmins, 1987). However, as the canopy gradually re-forms, both light intensity and nutrient availability decline (Kimmins, 1987). Understory plant species that occupy these sites during this transition must therefore have wide adaptability to environmental conditions. A plant's ability to adapt to these changes is partly related to its biomass allocation pattern.

The distribution of biomass among plant organs is not fixed. It is affected by the environment, habitat of the plant, life span of the plant, competitive interactions and many other factors (Abrahamson, 1975; Abrahamson, 1979). Any growth limiting condition or resource will also induce a change in the resource partioning of the plant. (Abrahamson, 1979; Hunt and Nicholls, 1986). Under particular conditions, any shortfall from the innate growth potential of the species may be partially explained in terms of the total of and ratio between, above ground and below ground stress (Hunt and Nicholls, 1986). Plants increase their proportional biomass allocation to that part of the plant which draws most upon the growth limiting part of the environment (Hunt and Nicholls, 1986). Any increase in growth varies depending on the environment and the plants' innate ability to capture resources (Reekie and Bazzaz, 1987c) and rapidity of development can be viewed as an important competitive feature of a plant (Mooney, 1972). By understanding how different plants gain and allocate their resources in response to certain environmental conditions it is possible to predict plant success in a given environment (Mooney, 1972).

The grass Calamagrostis canadensis (Michx.) Beauv. (marsh reed grass) has been observed within all successional stages of forested sites but is most abundant when the forest canopy is removed. It is widely believed that rhizome recruitment and clonal spread from grass plants that exist prior to harvesting results in the dense grass coverage experienced on some cutblocks (Haeussler and Coates, 1986). As the canopy of a stand gradually rebuilds after a disturbance the growth rates and cover of C. canadensis have been found to decrease (Younkin, 1973; Eis, 1981). It is not clear, however, how the biomass allocation of marsh reed grass changes when grown under the extremely different environmental conditions of an open cutblock and a closed canopy forest.

In agronomic species, tiller and root production have been found to be promoted by increased light and nutrients (Evans et al., 1964; Laude, 1972; Lunt, 1972; Rogan and Smith, 1975; Grime, 1977; Williams, 1980; Redmann and Reekie, 1982; Vince-Prue and Canham, 1983), while nutrient deficiencies tend to promote rhizome growth in some of these plants (Evans et al., 1964; Rogan and Smith, 1975; Noble and Marshall, 1983). The impact of an interaction between light and nutrients on the biomass allocation of plants has yet to be thoroughly described.

Lovett-Doust (1987) found that the interaction between light and nutrients altered the growth of _Ranunuculus_ _repens_ L. by increasing structural growth to a greater extent when grown under high light and high nutrient conditions.

The objective of this study was to determine the biomass allocation pattern employed by _C._ _canadensis_ under different light and nutrient regimes in both greenhouse and field conditions.

METHODS and MATERIALS

A:

Seed from two populations of Calamagrostis canadensis, an upland population (36 km Southeast of Slave Lake, W 114^0 42′ N 55^0 19′) and a lowland population from the middle of a large wetland complex (3 km east of Slave Lake, Alberta) was collected in August of 1987. The seed was stored at -18^{o}C until May 20, 1988. To enhance germination, the seed of each population was then placed on wet paper towels in separate Spencer-Lemaire germinating trays. The trays were then stored at 3 to 5^{o}C for 14 days. Seeds were then germinated on moist potting soil in the Spencer-Lemaire germinating trays in a greenhouse.

A 2:1 sand:peat mixture was added to 108, 15 cm diameter pots. On June 10, germinates from each population were placed into separate pots (54 pots for each population). A one-week establishment period with full greenhouse light and daily watering was used to ensure establishment of at least one germinate in each pot. On June 17, 1988 the germinates were thinned to one per pot and the light treatments started.

Two experimental blocks were established at different locations within the greenhouse. Each population was divided into three groups; high (full greenhouse light), medium (45% full light), and low light (15% full light). These light levels were to correspond, respectively, to the light levels present in a clearcut, a partially closed deciduous crown, and a fully closed spruce crown (Kimmins, 1987). The light levels were achieved through the layering of plastic shade screen on all sides of wooden frames (100 x 60 x 90 cm high). Light quality underneath the shade screens was not determined.

Within each light enclosure pots were divided into three nutrient treatments; high, medium, and low. The nutrients were applied with 100ml of water every third day, at a rate of 300 mg, 100mg, and 0 mgs, respectively of a 20 - 20 - 20 (N-P-K) fertilizer complete with micronutrients. This rate of fertilizer application ensured the replacement of nutrients in the rooting zone lost due to watering between nutrient treatments. Pots were watered every day until soil saturation. This ensured that moisture stress was not significant during the experiment and nutrient levels did not build within each pot. All plants were grown at an average temperature of 22^{O}C and under an 18 hour photoperiod.

The experiment ran for 62 days and was harvested on August 17, 1988. This is close to the natural growing period of the plant, plus the plants in the full light treatment were beginning to require watering more than once per day. At harvest, the number and length of tillers for each plant was measured. Soil was washed from below ground parts of the plants and the rhizomes were removed and counted. The plants were then dried at 70^{O}C for 2 days and dry weights of the tillers, rhizomes and roots were recorded. From these the rhizome:tiller, root:shoot, and below ground:above ground ratios were calculated. These values were analyzed using a complete factorial ANOVA design (SPSSx) with linear and polynomial derivations of the main effects (Mize and Schultz, 1985). Data from the experimental blocks were grouped together for analyses because there were no significant differences between them.

B:

Sods of C. canadensis were collected from the Calling Lake, Alberta area (W 113° 08′ N 55° 13′) in mid-August. From two twenty point transects underneath three different canopy closures, ten 275 cm^2 sods were randomly collected.The crown closures were visually estimated to be approximately 0% (clearcut four years earlier), 40% (twenty year old harvest site), and 85% (mature spruce forest). All C. canadensis rhizomes and tillers were removed from each sod and the average rhizome diameter for each sod was determined and recorded. Rhizome and tillers were then dried at 70° C for 24 hours and weighed.

Total non-structural carbohydrate analysis of the rhizomes from each sod was performed following Smith (1981) as adapted by Hogg (unpublished) for C. canadensis. The rhizomes were ground to pass a 40 - mesh screen. Approximately 50 mg of the powdered material was placed into each test tube and mixed with 20 ml of distilled water. Test tubes were then capped and placed in boiling water for 1 1/2 hours. The solution was then vaccum filtered and transferred into 100 ml volumetric flasks and brought up to volume with distilled water. An 8.18 ml sample of each of these filtrates was placed with 0.91 ml of 1 N H_2SO_4 into test tubes. These were heated in a boiling bath for 20 minutes, then cooled and neutralized with 0.91 ml of 1 N NaOH. At this point a water blank of 10 ml of distilled water and a fructose standard of 2 ml of fructose (1 g/l) with 8 ml of distilled water was included. Ten ml of Reagent 50 was added to each test tube, which was then placed back into the boiling bath for another 20 minutes. When the test tubes were removed from the boiling bath 2 ml of potassium iodide - potassium oxalate solution, followed by 10 ml of 1 N H_2SO_4 and 0.25 ml of gelatinized starch solution was added to each. This mixture was then titrated with 0.02 N sodium thiosulfate until the solution colour changed to a pale blue. The percentage of non - structural carbohydrates in each sample was calculated with the following formulas: $TNC = d * F * (Tw - Tu)/(Tw - Tt)$

$\%TNC = 100 * TNC/W$

where TNC: Total nonstructural carbohydrates in sample

d: Dilution factor (100/8.18)

F: mg of fructose in standard (2.0 mg)

Tw: Titration of water blank

Tu: Titration of sample

Tt: Titration of fructose standard

W: Dry weight of sample.

The data was analyzed using a one-way ANOVA with polynomial derivations of the main effect (SPSSx). Since there was no statistical difference between transects they were combined in the analysis.

RESULTS

A:

The greatest impact of light and nutrient availablity was on tiller production of the grass plants. Numbers of tillers produced increased with increasing light intensity and nutrient availability in both the upland and lowland population (Fig. 2-1). However, the increases associated with light had a significant quadratic effect (Table 2-1), suggesting the high light intensity had a much larger effect than the lower light intensities. The population x light x nutrient interaction was also significant (Table 2-1). This relates to greater tiller production of the upland population in the high light and nutrient treatments.

Average tiller length generally increased with the higher light and nutrient levels (Fig. 2-2). Increases as a result of nutrient availability, however, had a significant quadratic effect (Table 2-1) suggesting that tiller length became constant at higher nutrient levels (Fig. 2-2). There was a significant interaction between light and nutrients (Table 2-1). At low nutrient levels (0g/l) the medium light treatment (45% full light) resulted in longer tillers than either the high or low light levels. Tiller lengths of the lowland population were longer than in the upland population under the high and medium light treatments as indicated by a significant population x light interaction (Table 2-1).

In both populations, total tiller weight increased with the higher light and nutrient levels (Fig. 2-3). However, the significant quadratic effect of light on tiller weight (Table 2-1) suggests that tiller weight tended to level off beyond 45% of full light. There was little effect of the nutrient treatment at low light intensities compared to the strong effect of nutrients at high light intensities (see significant light x nutrient interaction, Table 2-1). Tillers produced by the lowland population were significantly heavier than tillers produced by the upland population under all treatments (Table 2-1; Fig. 2-3).

Both populations generally increased rhizome number production with increased nutrient availability and light intensity (Fig. 2-4). However, rhizome production levelled off and even decreased (in the lowland population, Fig. 2-4), as nutrient availability increased (see the significant quadratic effect for the nutrient treatment and the significant population x light x nutrient interaction Table 2-1). However, there were no significant differences between populations (see main effects, Table 2-1).

Generally rhizome weight increased with greater light and nutrient levels (Fig. 2-5). Light, however, had a significant quadratic effect on rhizome weight (Table 2-1). Rhizome weight was low under both the low and moderate light intensities but much greater under high light intensity. The light by nutrient interaction generally related to the greater response of the higher nutrient treatments only at the highest light intensity (Fig. 2-5). This suggests that any increase in rhizome weight associated with higher nutrients will only occur under high light intensities.

In both populations, root mass was greatest at higher light intensities (Fig. 2-6). However, there was a significant quadratic effect on root weight associated with both light and nutrient levels (Table 2-1). Under the nutrient treatment, root weight leveled off and even decreased (in the lowland population, Fig. 2-6) as nutrient availability increased. For the light treatments, only the high light had a high root mass. However, root weight was also altered by the interaction between population x light x nutrient (Table 2 - 1). Root production under low light and nutrient levels in both populations was minimal, while root production under high and medium light and nutrient treatments was greater in the lowland population than in the upland population (Fig. 2-6).

There was no impact of population on root:shoot ratios (Table 2 - 1). With both high light and nutrient treatments, there was a low root:shoot ratio (Fig. 2-7). Nutrient level, however, had a significant quadratic effect on root:shoot ratio; low nutrient levels had a high root:shoot ratio followed by a sharp reduction in the ratio at higher nutrient treatments (Fig. 2-7). There was also a significant light and nutrient interaction effect on root:shoot ratio (Table 2-1). At low nutrient levels the proportion of biomass allocated to the roots greatly increased with light intensity (Fig. 2 - 7). However, this was not so at the higher nutrient levels. This trend was generally similar in the above ground:below ground ratio, with the exception that the populations were significantly different (Table 2-1; Fig. 2-8). The lowland population allocated more biomass to its below ground organs than the upland population (Fig. 2-8).

There was a significant increase in rhizome:tiller ratio with increasing light intensities (Table 2 - 1; Fig. 2-9) but there was no effect of nutrient treatment. The lowland population had higher proportionate rhizome production than the upland population (Table 2-1).

B:

As crown closure increased there was a corresponding linear decrease in rhizome (Fig. 2-10; Table 2-2) and tiller dry weights (Fig. 2-11; Table 2-2), rhizome diameter (Fig. 2-12; Table 2-2), and in the percentage of non-structural carbohydrates contained in the rhizomes (Fig. 2-13; Table 2-2). However, the grass growing under the 40% crown closure canopy allocated proportionately more biomass to rhizomes than the grass grown under the other two crown closures (Fig. 2-14; note the significant quadratic effect, Table 2-2).

DISCUSSION

As light intensity and nutrient availability increased in the greenhouse experiment there was generally an increase in numbers and size of tillers, roots and rhizomes of C. canadensis. In other species, this has also been observed for tillers, roots (Evans et al., 1964; Anderson et al, 1969; Laude, 1972; Lunt, 1972; Mooney, 1972; Rogan and Smith, 1975; Grime, 1977; Williams; 1980; Redmann and Reekie, 1982; Vince-Prue and Canham, 1983), and rhizomes (Palmer, 1958; Bazzaz and Reekie, 1985; Kigel and Koller, 1985). With C. canadensis, however, for nutrient availability to have any impact on plant growth, moderate to high light intensities were required. Under low light conditions growth was limited in all nutrient treatments and only when light intensity increased did nutrient availability become a growth limiting factor. Similarily this was observed with Ranunculus repens (Lovett-Doust, 1987) and other grass species (Laude, 1972). A large reduction in light intensity resulted in reduced biomass production in all C. canadensis plant structures. However, biomass was mostly directed towards tillers under low light intensities. Presumably photosynthetic area is most limiting to growth under low light and the plant is allocating more of its energy to the growth limiting part of the environment (Hunt and Nicholls, 1986).

Increases in light intensity and nutrient availability promote greater rhizome growth in C. canadensis. The strategy of increasing rhizome production in response to nutrient deficiencies (Evans et al, 1964; Rogan and Smith, 1975; Noble and Marshall, 1983), as found in the greenhouse experiment, or low light levels, as found in the field experiment, is brought about by increasing the number of rhizomes produced and proportional biomass allocated to rhizome material, while not increasing the total non-structural carbohydrate content of the rhizomes. This increases the probability of contact with a better growing site but reduces the carbohydrate cost if that rhizome does not come into contact with a better site. Cook (1983) and Loehle (1987) both stated that stolons are capable of detecting gradations of nutrients in the soil and establishing ramets in locations of higher nutrients. A plant which is growing in an extremely unfavourable site (ie: low nutrient and low light) has to expend all its energy on the production of organs that will ensure survival in the short term (roots or tillers). It is only when survival is ensured that the plant can start to produce rhizomes and search for a new growing site.

Assuming that light intensity and nutrient availability are highest in early successional/cut-block sites, C. canadensis would attain its greatest growth under these conditions. In these open sites rhizome production and spread would be very high, and the non-structural carbohydrates stored in these structures would be at a maximum. The rhizomes on these site would then, presumably, have a high regenerative capacity. Under a forest canopy, thus low light intensities and nutrient availabilities, this species would have low biomass production in all plant structures but particularily below ground structures. Any growth by the plant would be mostly directed towards structures to capture light.

The greenhouse experiment also indicated that the population from which the plant originated impacts biomass production. The lowland population was able to produce greater biomass in both below ground and above ground structures than the upland population. The proportional allocation of biomass to each structure, however, was generally the same in both populations.

The results of the first part of this study represent initial growth after germination and the pattern of biomass allocation portrayed may be essential for initial establishment on the site. During the first year of establishment the priority of growth under all conditions may be the productions of tillers. It can be hypothesised that plants germinating under medium light levels establish the numbers of rhizomes to promote a guerilla growth strategy but it is not until the following years that the proportional biomass allocation to the rhizomes increased to create the high rhizome:tiller ratios found under the medium closure canopy. Presumably, the plants found in the four year old clearcut (0% crown closure) produce high amounts of tiller material because the area had been nearly completely colonized and the only method of establishing new plants is through the production of tillers and seed. Plants grown under a closed canopy (85% crown closure), however, concentrate their efforts on tiller growth to promote and ensure the survival by allowing for sufficient net photosynthesis. Thus, in the growing seasons following establishment, the biomass allocation pattern must change in favour of rhizomes to allow for local spread of the plant until the site is competely colonized.

TABLE 2-1

SIGNIFICANCE OF F DERIVED THROUGH A FACTORIAL ANOVA WITH LINEAR AND POLYNOMIAL DERIVATIONS OF EACH MAIN EFFECT

EFFECT	NUMBER OF TILLERS	AVERAGE LENGTH TILLERS	TILLER WEIGHT	NUMBER OF RHIZOMES	RHIZOME WEIGHT	ROOT WEIGHT	ROOT: SHOOT RATIO	RHIZOME: TILLER RATIO	BELOW: ABOVE RATIO
POP.	0.991	0.000	0.002	0.082	0.075	0.000	0.079	0.038	0.038
LIGHT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
L*LIN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
L*QUAD	0.007	0.587	0.000	0.064	0.000	0.000	0.100	0.239	0.141
NUTRIENT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.433	0.000
N*LIN	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.217	0.000
N*QUAD	0.835	0.020	0.610	0.001	0.416	0.000	0.000	0.701	0.000
POP x LIG	0.000	0.004	0.059	0.010	0.393	0.008	0.119	0.513	0.116
POP x NUT	0.651	0.873	0.106	0.015	0.402	0.116	0.250	0.813	0.225
LIG x NUT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.340	0.000
P x L x N	0.003	0.604	0.174	0.049	0.515	0.027	0.223	0.951	0.214

POP = P = POPULATION
LIG = L = LIGHT
NUT = N = NUTRIENT
LIN = LINEAR EFFECT
QUAD = QUADRATIC EFFECT

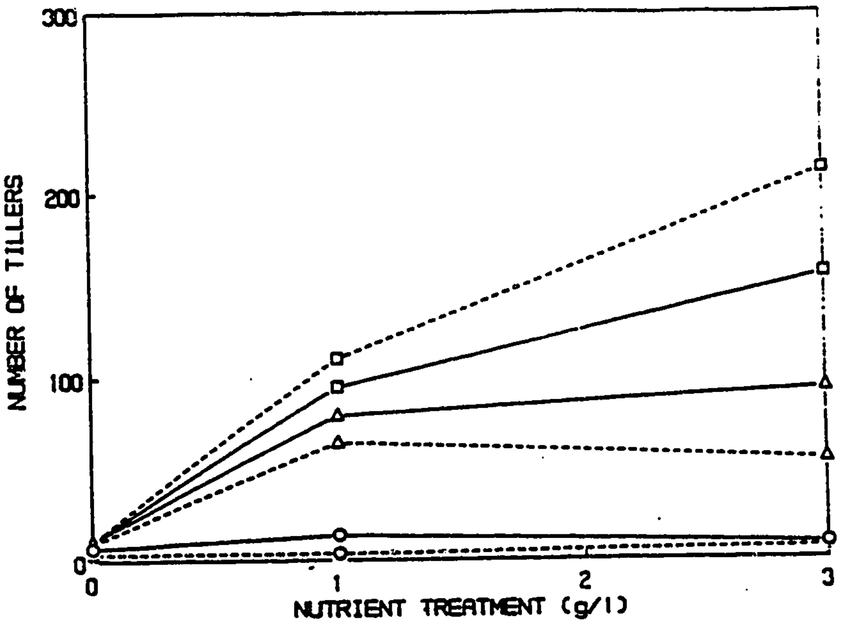
Probabilities determined through a factorial ANOVA with main effects showing polynomial derivations. Underlined values portray significant differences at $p<0.05$.

Table 2-2 SIGNIFICANCE OF F DERIVED THROUGH AN ANOVA WITH LINEAR AND POLYNOMIAL DERIVATIONS OF THE MAIN EFFECT.

PARAMETER	LINEAR AND POLYNOMIAL DERIVATIONS OF MAIN EFFECT	SIGNIFICANCE OF F
RHIZOME DRY WEIGHT		0.000
	LINEAR	0.000
	QUADRATIC	0.442
TILLER DRY WEIGHT		0.000
	LINEAR	0.000
	QUADRATIC	0.145
RHIZOME:TILLER RATIO		0.002
	LINEAR	0.125
	QUADRATIC	0.002
RHIZOME DIAMETER		0.000
	LINEAR	0.000
	QUADRATIC	0.073
NON-STRUCTURAL CARBOHYDRATE CONTENT OF RHIZOMES		0.000
	LINEAR	0.000
	QUADRATIC	0.617

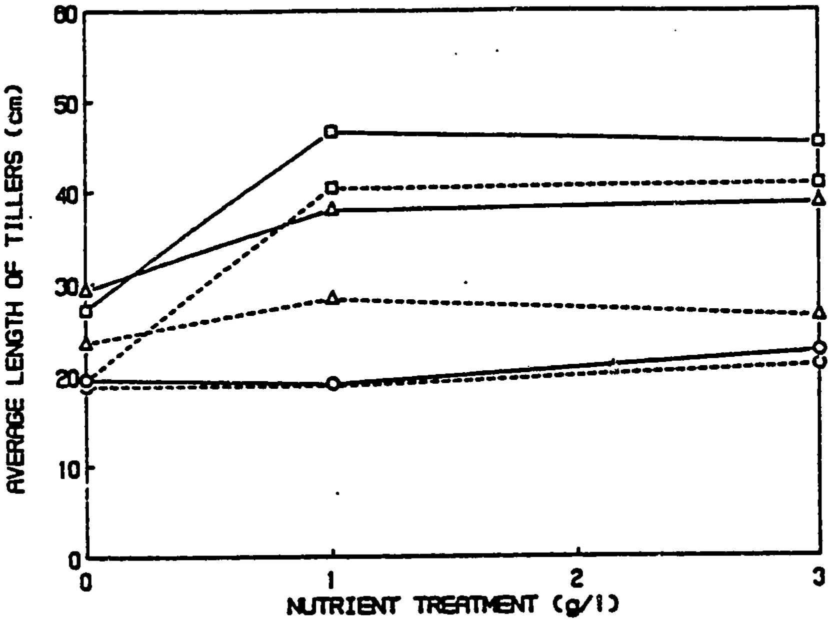
PROBABILITIES DETERMINED THROUGH A ONE-WAY ANOVA WITH POLYNOMIAL DERIVATIONS OF THE MAIN EFFECT FOR EACH PARAMETER.

FIG. 2 - 1 NUMBER OF TILLERS PRODUCED PER SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



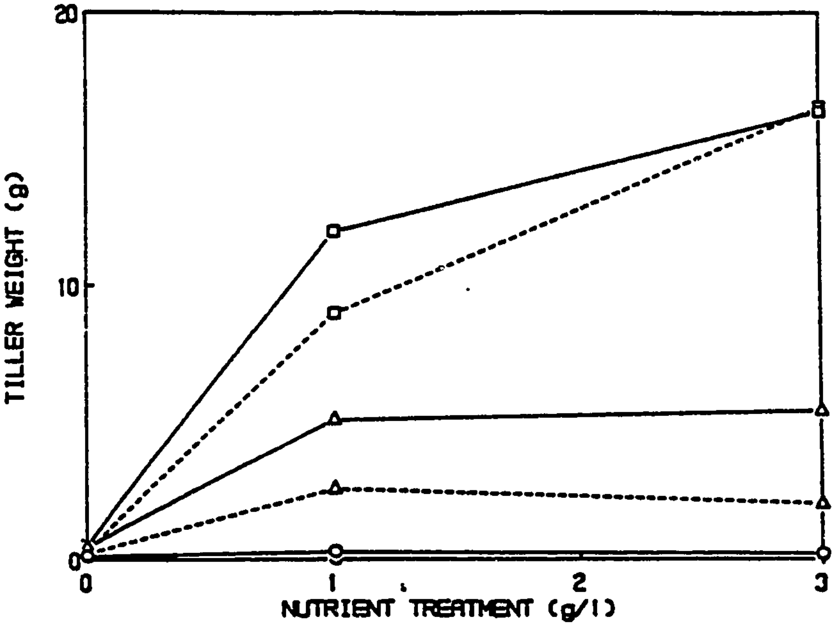
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 2 AVERAGE LENGTH OF TILLERS IN A GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



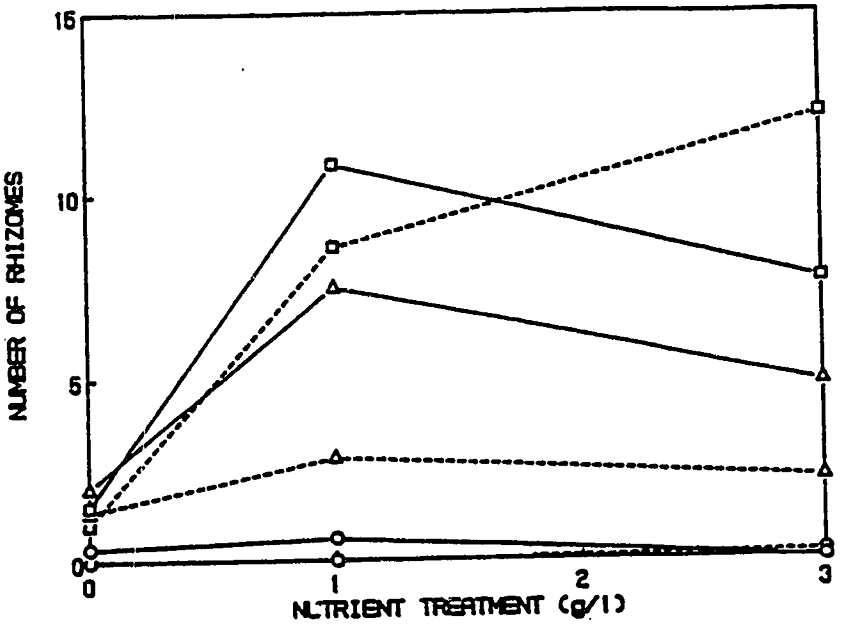
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 3 TOTAL TILLER WEIGHT PRODUCED BY A GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



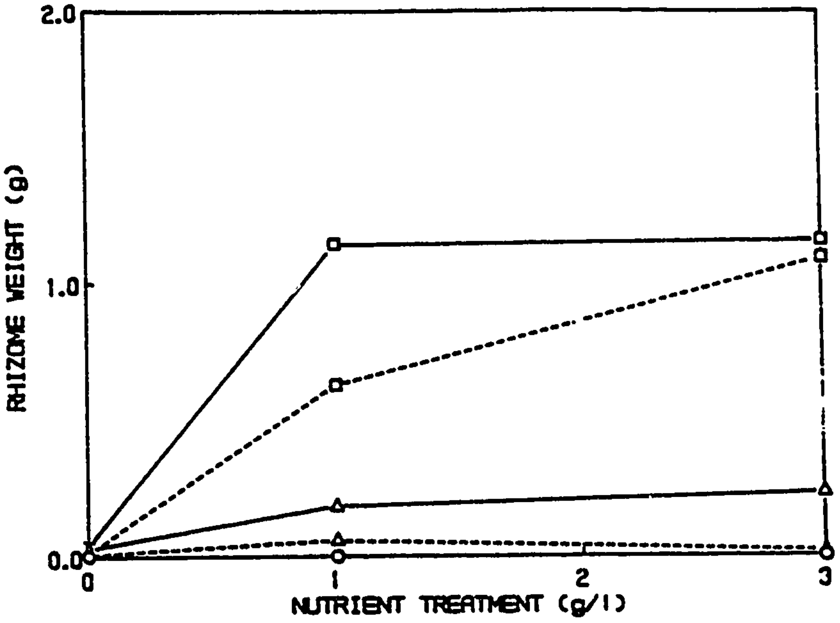
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 4 NUMBER OF RHIZOMES PRODUCED PER SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



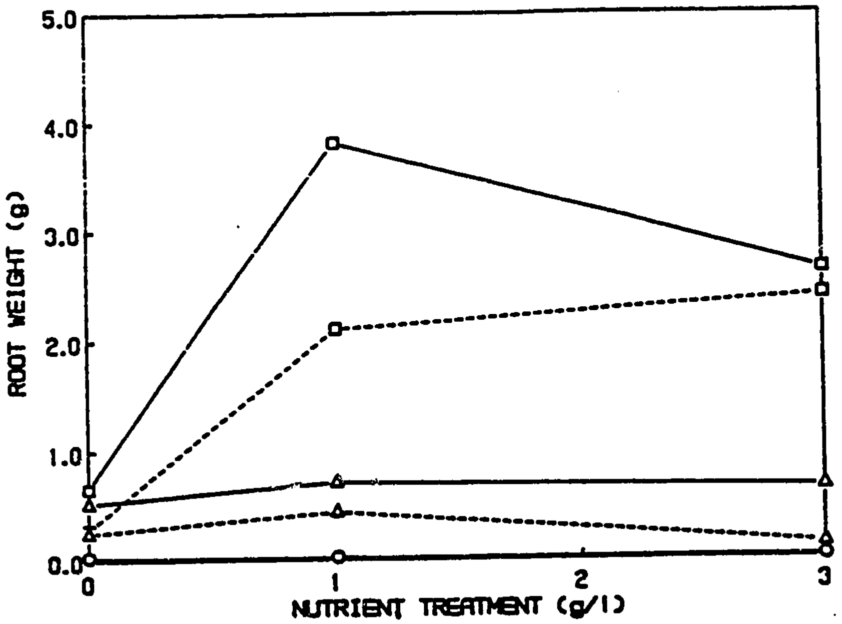
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 5 TOTAL RHIZOME WEIGHT PRODUCED BY A GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



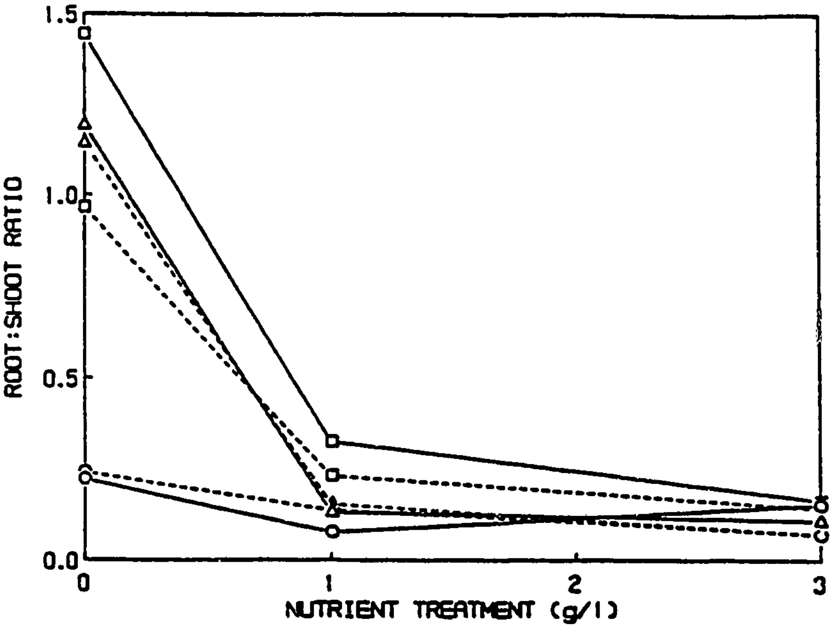
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 6 TOTAL ROOT WEIGHT PRODUCED BY A GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



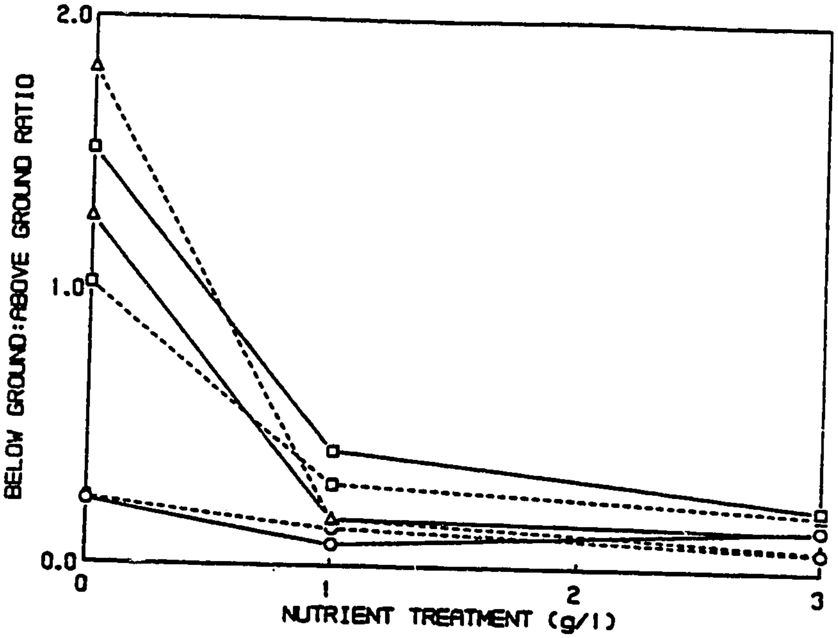
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 7 ROOT:SHOOT RATIO PER GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



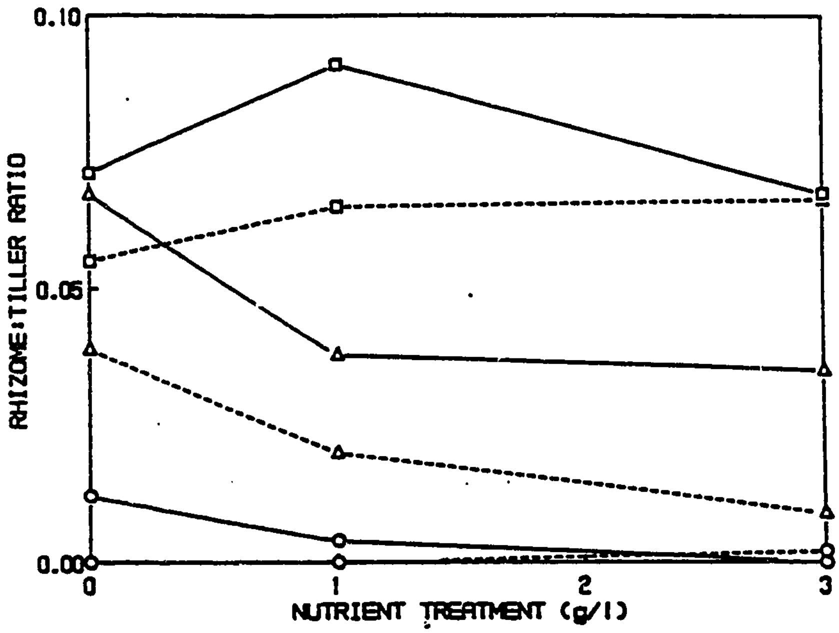
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 8 BELOW GROUND: ABOVE GROUND RATIO PER GRASS SWARD AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



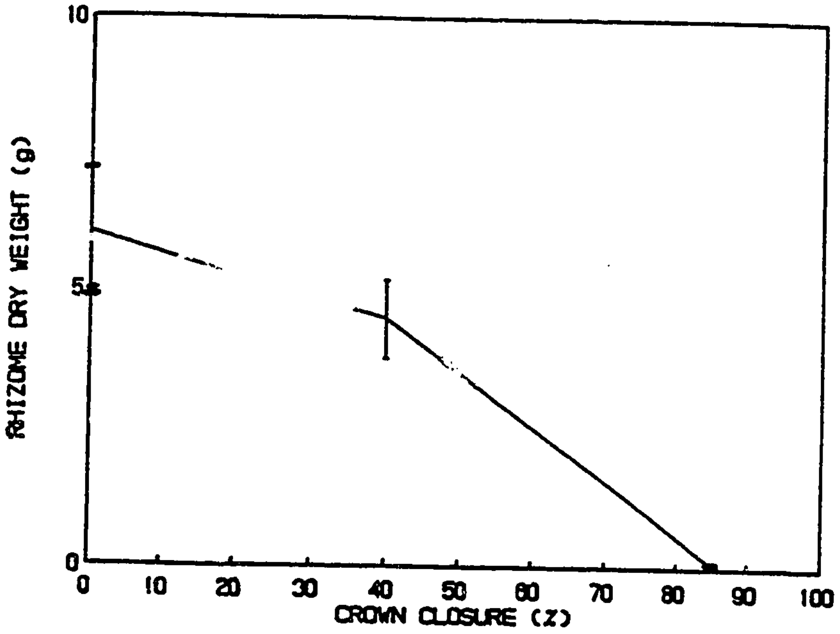
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 9 RHIZOME:TILLER RATIO PER GRASS SWARD PLOTTED AS A FUNCTION OF NUTRIENT LEVEL FOR THREE DIFFERENT LIGHT LEVELS FROM UPLAND AND LOWLAND POPULATIONS.



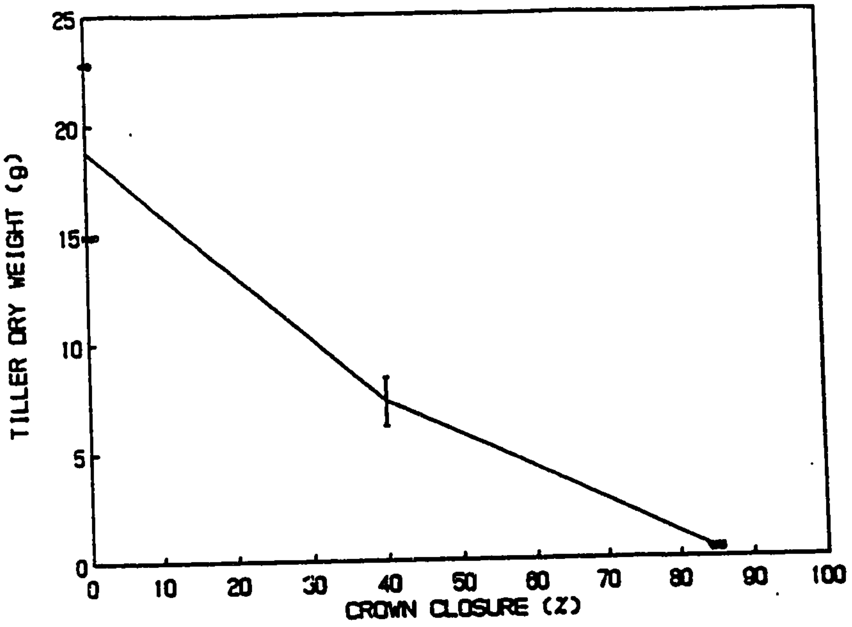
Circle indicates 15% full light, triangle indicates 45% full light, and square indicates full light. Solid line represents the lowland population and the dashed line represents the upland population.

FIG. 2 - 10 TOTAL RHIZOME DRY WEIGHT PRODUCED PER GRASS SOD AS A FUNCTION OF CROWN CLOSURE.



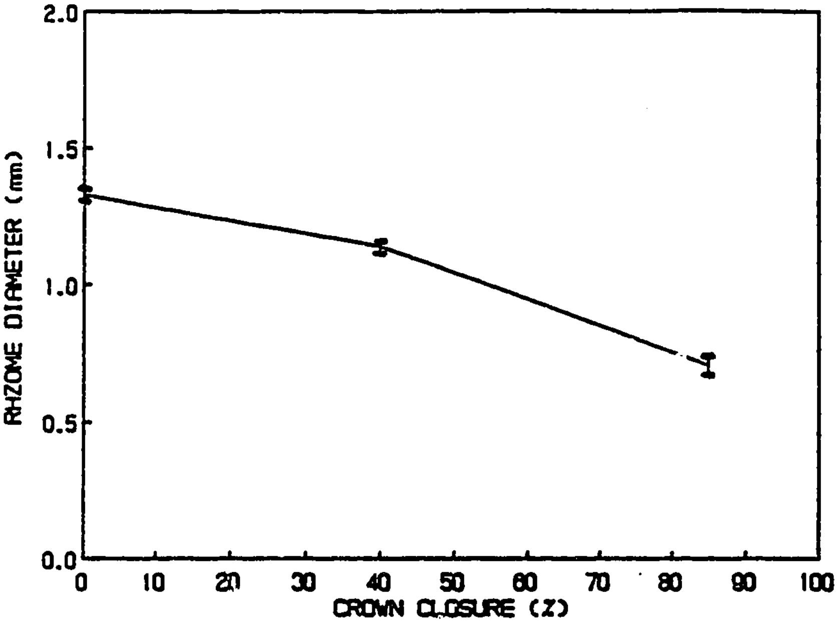
Vertical line indicates standard error.

FIG. 2 - 11 TOTAL TILLER DRY WEIGHT PRODUCED PER GRASS SOD AS A FUNCTION OF CROWN CLOSURE.



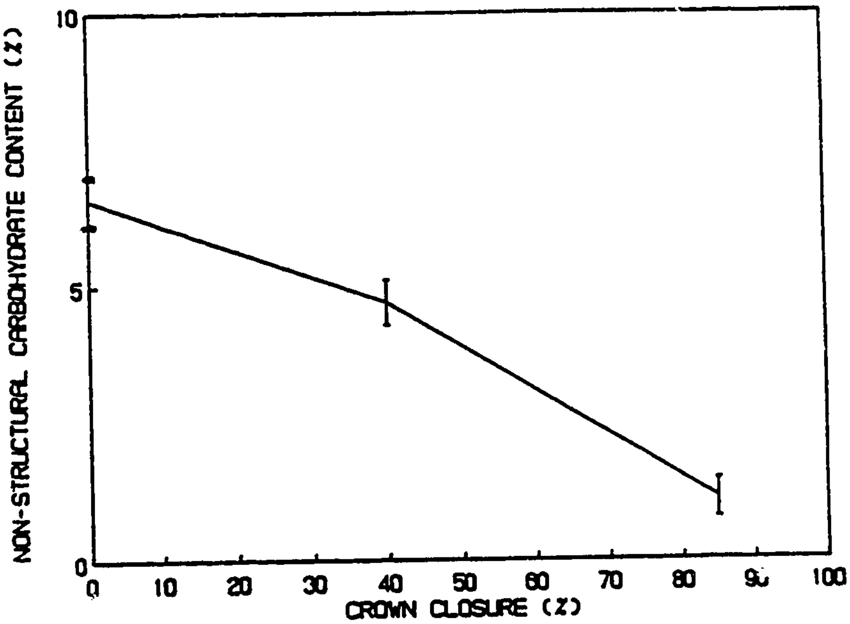
Vertical line indicates standard error.

FIG. 2 - 12 AVERAGE RHIZOME DIAMETER PRODUCED PER GRASS SOD AS A FUNCTION OF CROWN CLOSURE.



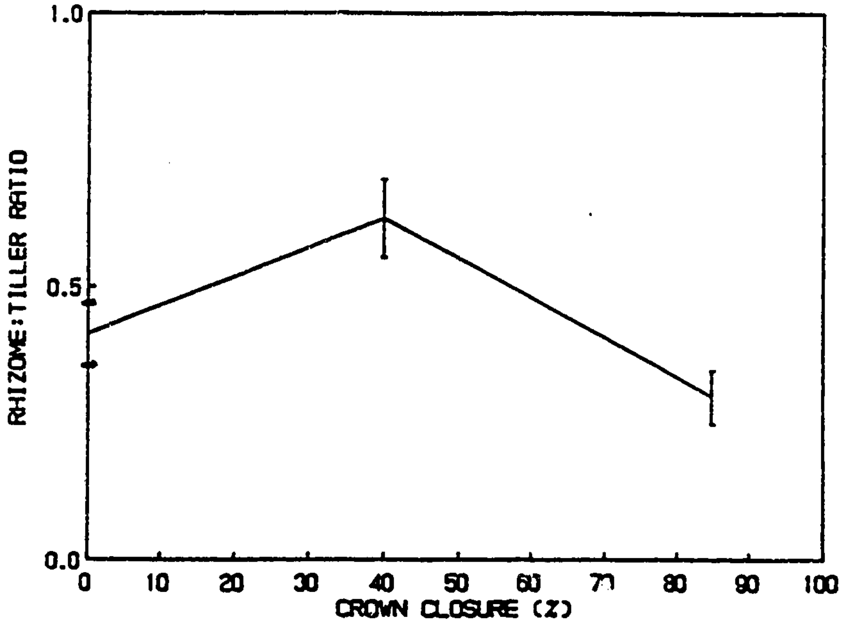
Vertical line indicates standard error.

FIG. 2 - 13 PERCENT NON-STRUCTURAL CARBOHYDRATE CONTENT OF RHIZOMES PRODUCED PER GRASS SOD AS A FUNCTION OF CROWN CLOSURE.



Vertical line indicates standard error.

FIG. 2 - 14 RHIZOME:TILLER RATIO PRODUCED PER GRASS SOD AS A FUNCTION OF CROWN CLOSURE.



Vertical line indicates standard error.

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Development of Dormant Calamagrostis canadensis buds on severed Rhizomes.

On wet mineral sites in the boreal forest of Western Canada, Calamagrostis canadensis (Michx.) Beauv. (marsh reed grass), is a widespread rhizomatous species which is very often abundant on forest cutblocks (Arlidge, 1967; Sims and Mueller-Dombois, 1968; Blackmore and Corns, 1979; Eis, 1981; Haeussler and Coates, 1986; Norokorpi, 1986). Site preparation of forest cutblocks is a forest industry activity which causes considerable physical disturbance of the rooting zone. It severs the rhizomes from the parent plant and may unintentionally spread them to new sites. This severing may either inhibit or promote the activation of dormant buds on the rhizome (Nyahoza et al 1974; Kigel and Koller, 1985). If rhizome severing promotes axillary bud development in marsh reed grass, then the disruption of the rooting zone during site preparation may enhance the rate at which this grass spreads and increase the total ground coverage by this species.

In Agropyron repens (L.) Beauv., which is somewhat similar in structure to C. canadensis, axillary buds are activated by fragmentation of the rhizome (McIntyre, 1969; McIntyre, 1970; McIntyre, 1971; McIntyre, 1972; Chancellor, 1974; Leakey et al. 1977b; Leakey et al, 1978a; Leakey et al., 1978b; Kigel and Koller, 1985). With A. repens, the presence of the rhizome apex on isolated rhizome segments has been found to inhibit development of axillary buds (McIntyre, 1969; Beasely, 1970; McIntyre, 1970; McIntyre, 1971;

McIntyre, 1972; Leakey et al., 1977b; Leakey et al, 1978a; Leakey et al., 1978b). Apical dominance in isolated rhizomes of this species has been assumed to be due to the inability of the axillary buds to effectively compete with the rhizome apex for a limited carbohydrate supply (McIntyre, 1969) and inhibition of the axillary buds is controlled by endogenous growth regulators orginating from both the parent plant and rhizome apex (Kigel and Koller, 1985). Excision of the rhizome apex releases the axillary buds from inhibition, however, a priority of axillary bud development is re-established (McIntrye, 1970). The fastest growing bud assumes dominance over the rest of the buds and eventually inhibits their growth (McIntyre, 1969; McIntyre, 1970; McIntyre, 1971; McIntyre, 1972; Chancellor, 1974; Leakey et al. 1977b; Leakey et al, 1978a; Leakey et al., 1978b; Kigel and Koller, 1985). This is characterized by tiller development being restricted to the buds nearest the apical end of the rhizome while buds furthest away from the apex produce rhizomes or remain inhibited (Beasely, 1970; McIntyre, 1970).

With A. repens rhizome buds adjacent to the rhizome apex were found to have the highest regenerative capacity. This was associated with their increased utilization of rhizome sugars (Leakey et al., 1977b). The regenerative capacity of rhizome buds adjacent to the parental base has not been thoroughly described. With C. canadensis, the response of axillary buds on rhizomes to severing and the priorty of bud development in relation to position and spatial orientation to the parent plant and rhizome apex is unknown. As well, most studies on dormant rhizome bud development have been conducted under dark conditions. This study, however, will approximate natural conditions by placing rhizomes in soil and having developed buds emerge into a full light environment.

The objectives of this study were to determine: 1) if buds from different rhizome positions have different potentials for initiation and tiller and rhizome production, 2) if the number of dormant buds on severed rhizome segments alters the potential for development of a single bud and 3) if the total non - structural carbohydrate content of rhizome segments differs over the length of the rhizome.

METHODS and MATERIALS

A:

Rhizomes were collected from a clearcut near Calling Lake, Alberta (W 113° 08′ N 55° 13′) on October 7th. These rhizomes were separated into two groups; rhizome segments adjacent to the parental base and segments adjacent to the rhizome apex. Segments contained five dormant buds. Buds were numbered according to their position in relation to the rhizome apex or the ramet base; position one was the bud closest to the rhizome apex or parental base and position 5 was the bud furthest from these points. Each position including the rhizome apex and parental base was severed at the mid-point between nodes, then measured for length and diameter. The segments were then dried at 70°C. for 24 hours then weighed. To gather sufficient tissue for analysis, segments were then randomly combined into groups of five of the same positional segments.

Total non - structural carbohydrate analysis of the rhizome bud positions was performed following Smith (1981) adapted by Hogg (unpublished). The nodal lengths of each position were ground to pass a 20 - mesh screen. Approximately 50 mg of the powdered rhizome was placed into each test tube and mixed with 20 ml of distilled water. Test tubes were then placed into boiling water for 1 1/2 hours. The solution was then vaccum filtered and transferred into 100 ml volumetric flasks and brought up to volume with distilled water. An 8.18 ml sample of each of these filtrates was placed with 0.91 ml of 1 N H_2SO_4 into test tubes. These were heated in a boiling bath for 20 minutes, then cooled and neutralized with 0.91 ml of 1 N NaOH. At this point a water blank of 10 ml of distilled water and a fructose standard of 2 ml of fructose (1 g/l) with 8 ml of distilled water was included. Ten ml of Reagent 50 was added to each test tube, which was then placed back into the boiling bath for another 20 minutes. When the test tubes were removed from the boiling bath 2 ml of potassium iodide - potassium oxalate solution, followed by 10 ml of 1 N H_2SO_4 and 0.25 ml of gelatinized starch solution was added to each. This mixture was then titrated with 0.02 N sodium thiosulfate until the solution colour changed to a pale blue. The percentage of non-structural carbohydrates in each sample was calculated with the following formulas: $TNC = d * F * (Tw - Tu)/(Tw - Tt)$

$$\%TNC = 100 * TNC/W$$

where TNC: Total non-structural carbohydrates in sample
d: Dilution factor (100/8.18)
F: mg of fructose in standard (2.0 mg)
Tw: Titration of water blank
Tu: Titration of sample
Tt: Titration of fructose standard
W: Dry weight of sample.

B:

Frozen sods of <u>Calamagrositis</u> <u>canadensis</u> were collected from the same clearcut near Calling lake, Alberta on March 25. In the laboratory, rhizomes were separated into two groups; rhizome segments adjacent to the parental base and segments adjacent to the rhizome apex (Fig. 3-4). Each rhizome group was sub-divided into classes based on the number of nodes each length contained. The nodal classes were from 1 bud per rhizome length up to 5 buds per rhizome length (Fig. 3-1). The shorter rhizomes always started from the base or apex position. Two additional classes of 5 buds plus the apex and 5 buds plus the base were included. Buds within each class were numbered according to their position in relation to the rhizome apex or the ramet base; position one was the bud closest to the rhizome apex or parental base and position 5 was the bud furthest from these points. Each rhizome series was replicated 6 times within two experimental blocks.

Trays 175 x 100 x 17 cm deep were divided into 6, 29 x 100 cm compartments and filled with potting soil. The six rhizome lengths of each rhizome series, of the two types, were planted 1 cm deep and grown for a period of 46 days. Standing water 2 cm deep was maintained in each tray during the experiment to maintain a constant soil moisture content. At completion each rhizome length was harvested and the number of buds that expanded, the resulting structure, its position on the rhizome nodal sequence, the dry weight of resulting structures, and the numbers of resulting structures on the original rhizomes were recorded. The frequency of bud development and position on the orignal rhizome length were determined.

These experiments were carried out in a greenhouse with an average temperature of 22^{0}C and a 18 hour photoperiod. The data were analyzed using the X^2 test of homogeneity, one-way ANOVA (SPSSx) and multiple comparison of means (BIOM). Since there were no statistical differences between blocks they were combined in the analysis.

RESULTS

A:

Internodal length generally increased with distance from both the rhizome apex and parental base (Fig. 3-2). Generally there was no difference in internode lengths between the rhizome apex and parental base segments ($p>0.200$; t-test). Also, there were no significant differences in the diameter of nodal segments adjacent to the rhizome apex (Table 3-1; Fig. 3-3), while the diameter of the base segments increased with distance from the parental base (Table 3-1). However, these were not significantly different by multiple comparison of means (Fig. 3-3). Diameter of nodal segments adjacent to the parental base were smaller than those of the segments adjacent to the rhizome apex ($p<0.05$; t-test).

The mean weight of individual nodal segments increased with distance from the parental base (Table 3-1; Fig. 3-4). There was, however, no difference in the mean weight of nodal segments leading up to the rhizome apex (Table 3-1). Nodal segments adjacent to the parental base were significantly lighter ($p<0.001$; t-test; Fig 3-4) and had lower concentrations of total non-structural carbohydrates ($p<0.001$; t-test; Fig. 3-5) than the segments adjacent to the apex. The non-structural carbohydrate content gradually increased with distance from the parental base, while there was no difference in non-structural carbohydrate content between nodal positions leading up to the rhizome apex (Fig. 3-5).

B:

As a group, buds on rhizome segments adjacent to the parental base had a significantly lower frequency of development than the buds on segments adjacent to the rhizome apex ($p<0.005$; X^2-test; Fig. 3-6). On rhizome segments with the apex excised, the greater the number of nodal buds on the rhizome segment the higher the total frequency of bud development ($p<0.005$; X^2-test; Fig 3-6). It was only positions 1 and 2 that experienced an increase in developmental frequency (Table 3-2; see vertical columns, "POSITIONS", Fig. 3-6). However, on rhizome segments with the parental base excised, there was no difference in total frequency of bud development with different numbers of nodes and buds ($p>0.95$; X^2-test). In this case the development of position 1 increased in frequency (Table 3-2, see vertical columns, "POSITIONS", Fig. 3-6) but did not alter overall total bud development on the rhizome segments

In terms of priority of development of buds of particular rhizome positions within nodal segments (see horizontal columns, "NODES PER SEGMENT", Fig. 3-6), when there were two buds on rhizome segments adjacent to the parental base either bud had nearly an equal probability of developing (Table 3-3; Fig. 3-6). When three or more buds were present on the parental base rhizome segments, however, the frequency of development of position 1 was greater than positions 2 or 3 and the last two positions on the segments did not develop at all (Fig. 3-6). Generally, when the parental base was not excised it was the only position to develop with the few exceptions where positions four and five developed (Table 3-3, Fig. 3-6). On rhizome segments adjacent to the apex the frequency of development for each position was not affected by the number of buds present on the rhizome segment (Table 3-3; Fig. 3-6). However, when the apex was attached, the apex and the bud furthest from the apex had the higher frequency of development (Table 3-3; Fig 3-6).

The following is an analysis of the strategy and performance of those buds which broke dormancy. Generally on both the apex and base segments there was little difference in the number of tillers per bud (Fig. 3-7), weight of tillers (Fig. 3-8), rhizomes per bud (Fig. 3-9), and weight of rhizomes (Fig. 3-10) in relation to position on the rhizome sequence (Table 3-4) or number of buds on the rhizome (Table 3-5). The proportional allocation of biomass between the rhizomes and tillers was also not affected by position or the number of buds on the rhizome segment (Fig. 3-11). The exception was on nodal segments adjacent to the parental base with three nodes per segment. In this case position 1 produced significantly more tillers (Table 3-4; Fig. 3-7) and rhizomes per bud (Table 3-4; Fig. 3-9), and had a proportionatley higher rhizome production (Table 3-4; Fig. 3-11) than position 2. The weight of the tillers produced by each position on this rhizome segment was also shown to be significantly different (Table 3-4), however, the multiple comparison of means did not show any difference between positions (Fig. 3-8).

When the rhizome apex was left attached the axillary buds produced fewer tillers (Fig. 3-7) and allocated proportionately more biomass to new rhizomes (Fig.3-11) than when the apex was excised. The analysis of variance did not detect a significant difference between positions (Table 3-4). However, the multiple comparison of means determined that the number of tillers produced at the apex was greater than that of the axillary buds (Fig. 3-7; Fig. 3-11). When the parental base was attached only position 4 had greater numbers of rhizomes than the other positions (Fig. 3-9). However, there was no significant difference in the proportional allocation of biomass to these rhizomes (Fig. 3-10).

DISCUSSION

Internodal length increased with distance behind the rhizome apex and parental base. However, rhizome segments adjacent to the apex had a greater diameter, weight and total non-structural carbohydrate content than the segments adjacent to the parental base. This suggests that non-structural carbohydrates were transported towards and stored near the rhizome apex at the expense of rhizome segments near the parental base. Presumably, the main function of rhizome segments adjacent to the parental base is to act as a transport channel for carbohydrates and not as a propagating unit. The high non-structural carbohydrate content of rhizome segments near the apex compared to the segments near the base probably accounts for the higher frequency of bud development on segments adjacent to the rhizome apex (Leakey et al., 1977b).

It should be noted, however, that when the base was excised, buds closest to this point were more likely to develop, presumably at the expense of buds on more distal segments which had a higher non-structural carbohydrate content. This implies that hormonal control of bud development in these segments must exist. Rogan and Smith (1976) suggested that in _A_. _repens_ a continuous supply of gibberellins from the parent plant was essential to maintain axillary bud inhibition. When the parental base of _C_. _canadensis_ was removed the bud closest to this point was the first to be released from inhibition. When this bud was released from dormancy, its growth suppressed the rest of the axillary buds. However, when there was short rhizome segments with few buds adjacent to the parental base, a marked priority of positional development did not arise because all buds on these segments are close enough to the parental base to be released from inhibition when the parental base is removed.

This response, however, does not occur in the carbohydrate rich apex segments of C. canadensis. Rhizome segments adjacent to the apex may be far enough from the parental base that the concentration of gibberellins is too low to have an effect on axillary bud development. When the apex of A. repens is left attached, NAA (1-naphthyl acetic acid) originating from the apex maintains a weak control over axillary bud development (Meyer and Buchholtz, 1963. Leakey and Chancellor, 1975). It appears, however, that C. canadensis has less apical dominance than A. repens. The excision of the C. canadensis rhizome apex removes any inhibition of the axillary buds and no priority of bud development arises. A formation of dominance amongst buds upon a rhizome segment leads to a more efficient use of resources (Harris and Davy, 1986).

The lack of dominance amongst the rhizome buds adjacent to the apex may be due to the depth of planting. Rhizome segments may be shallow enough that shoots reached the light before any bud inhibition could occur. Harris and Davy (1986) found that at lesser planting depths shoots originating from Elymus farctus (Viv.) rhizome segments were able to reach the light and achieve independence before bud inhibition could occur. Presumably, then the non-structural carbohydrate-rich apex segments of C. canadensis had enough stored energy to overcome the planting depth used in this experiment. It could be argued then that the non-structural carbohydrate-poor parental base segments formed a priority of bud development to better utilize the resources present to overcome the planting depth. Planting depth in this experiment, however, was certainly within the range of rhizome depth in natural sites.

The presence of the rhizome apex or parental base suppresses the development of the buds on their adjoining rhizomes. Retention of the growing point (either the parental base or rhizome apex) allows for the construction and transport of substances which dictate the priority of bud development and allocation of non-structural carbohydrates (Kigel and Koller, 1985). It can be assumed then that each bud is equally predisposed to develop and it is only when the growing point is retained or when concentrations of endogenous growth regulators are high, that priority of bud development can occur.

The lack of significant difference between the structural development of the buds after they had been released from inhibition suggests that once a developed bud emerges from the soil it likely produces a certain number of tillers and rhizomes irregardless of its position on the rhizome segment or the number of buds on the segment. Presumably then, the post-emergent condition of the environment, and not the total non-structural carbohydrate content of the originating rhizome, must dictate tiller and rhizome production of the developed bud. Therefore only the initiation of the dormant buds may be affected by its position on the orginating rhizome while development of that position is limited by the condition of the post-emergent environment.

TABLE 3-1 PROBABILITIES OF SIGNIFICANT DIFFERENCES AMONG THE FIVE NODAL SEGMENTS ADJACENT TO THE APEX AND SECONDLY AMONG THE FIVE NODAL SEGMENTS ADJACENT TO THE PARENTAL BASE.

CHARACTERISTICS OF NODAL SEGMENTS	APEX SEGMENTS	BASE SEGMENTS
LENGTH	0.0002	0.0000
DIAMETER	0.5117	0.0271
WEIGHT	0.9849	0.0000
TOTAL NON-STRUCTURAL CARBOHYDRATE CONTENT	0.9627	0.0289

PROBABILITIES DERIVED FROM A ONE-WAY ANOVA.

TABLE 3-2 PROBABILITY OF SIGNIFICANT DIFFERENCES IN FREQUENCY OF DEVELOPMENT AMONG CORRESPONDING POSITIONS ON RHIZOME SEGMENTS CONTAINING DIFFERENT NUMBERS OF NODES PER RHIZOME SEGMENT. (SEE VERTICAL COLUMNS, 'POSTIONS', FIG. 3-6)

POSITION	APEX SEGMENTS	BASE SEGMENTS
1	0.025	0.005
2	0.025	0.500
3	0.900	0.100
4	0.500	0.975
5	0.900	0.500

PROBABILITIES WERE DETERMINED THROUGH THE USE OF X^2 TEST OF HOMOGENEITY.

TABLE 3-3 PROBABILITIES OF SIGNIFICANT DIFFERENCES IN THE FREQUENCY OF DEVELOPMENT OF BUDS COMPARING DIFFERENT BUD POSITIONS ON THE SAME RHIZOME SEGMENT. (SEE HORIZONTAL ROWS, 'NODES PER SEGMENT', FIG. 3-6)

NODES PER SEGMENT	APEX SEGMENTS	BASE SEGMENTS
2	0.500	0.500
3	0.975	0.500
4	0.100	0.010
5	0.500	0.005
APEX/BASE	0.025	0.005

PROBABILITIES WERE DETERMINED THROUGH THE USE OF X^2 TEST OF HOMOGENEITY.

TABLE 3-4 PROBABILITY THAT DIFFERENT BUD POSITIONS ON THE SAME RHIZOME SEGMENT WERE SIGNIFICANTLY DIFFERENT (SEE HORIZONTAL ROWS, NODES PER SEGMENT, FIG. 3-7 TO 11).

NODES PER RHIZOME	NUMBER OF TILLERS		NUMBER OF RHIZOMES		RHIZOME WEIGHT		TILLER WEIGHT		RHIZOME: TILLER RATIO	
	APEX	BASE	APEX	BASE	APEX	BASE	APEX	BASE	APEX	BASE
1	------	------	------	------	------	------	------	------	------	------
2	0.2500	0.2500	0.2500	0.2500	0.2500	0.2500	0.2500	0.2500	0.2500	0.2500
3	0.6368	0.0257	0.8923	0.0075	0.4633	------	0.4925	0.0243	0.6212	0.0006
4	0.2383	0.1313	0.8070	0.9928	0.6333	------	0.6611	0.2055	0.4243	0.5134
5	0.3444	0.4557	0.7453	0.1477	0.1000	0.2333	0.3103	0.0448	0.3553	0.4870
APEX/BASE	0.1982	0.5245	0.6567	0.0054	0.6016	------	0.3648	0.7699	0.4753	0.0730

Probabilities of F determined through one-way ANOVA. Blank space indicates that not all positions on the rhizome segment produced new rhizomes.

TABLE 3-5 PROBABILITY THAT THE SAME BUD POSITION ON RHIZOMES CONTAINING DIFFERENT NUMBERS OF DORMANT BUDS WERE SIGNIFICANTLY DIFFERENT (SEE VERTICAL COLUMNS, POSITIONS, FIG. 3-7 TO 11).

POSITION	NUMBER OF TILLERS		NUMBER OF RHIZOMES		RHIZOME WEIGHT		TILLER WEIGHT		RHIZOME: TILLER RATIO	
	APEX	BASE	APEX	BASE	APEX	BASE	APEX	BASE	APEX	BASE
1	0.2500	0.2500	0.2500	0.2500	0.8812	0.2500	0.2500	0.1000	0.2500	0.2500
2	0.2500	0.2500	0.2500	0.2500	0.2251	0.2500	0.2500	0.2500	0.2500	0.2500
3	0.2241	------	0.5082	------	0.0150	------	0.3578	------	0.2952	------
4	0.7805	------	0.7250	------	0.6049	------	0.8155	------	0.0482	------
5	0.2721	------	0.5097	------	0.1357	------	0.0716	------	0.9730	------
APEX/BASE	------	------	------	------	------	------	------	------	------	------

Probabilities of F determined through one-way ANOVA. Blank space indicate positions with non-development of dormant rhizome bud.

FIG. 3-1 RHIZOME SEGMENTS NUMBERED STARTING FROM THE PARENTAL BASE AND IN REVERSE ORDER FROM THE RHIZOME APEX.

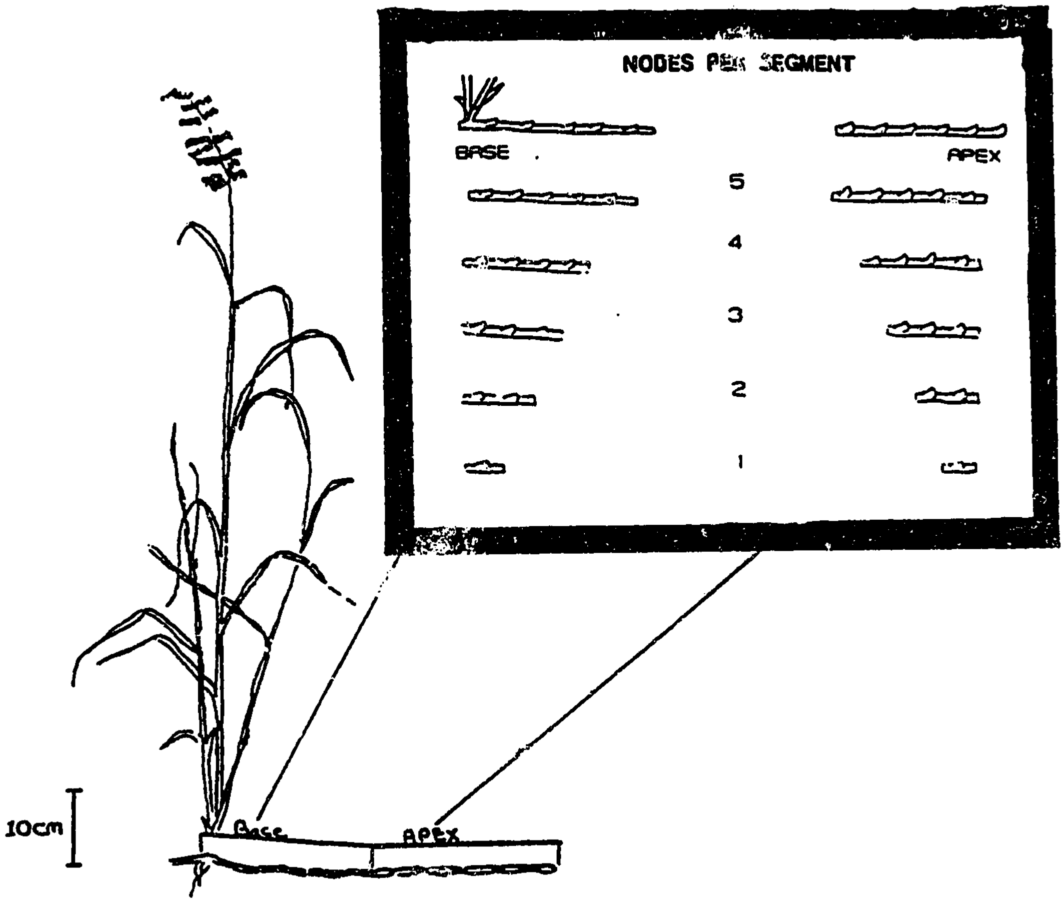


FIG. 3 - 2 LENGTH OF INTERNODE PLOTTED AGAINST POSITION ON RHIZOME FOR PARENTAL BASE AND RHIZOME APEX SEGMENT TYPES. 1-way ANOVA conducted (Table 3-1) and multiple comparison of means (T-K method) done separately on each rhizome segment type. Similar letters within each segment type denote no significant difference.

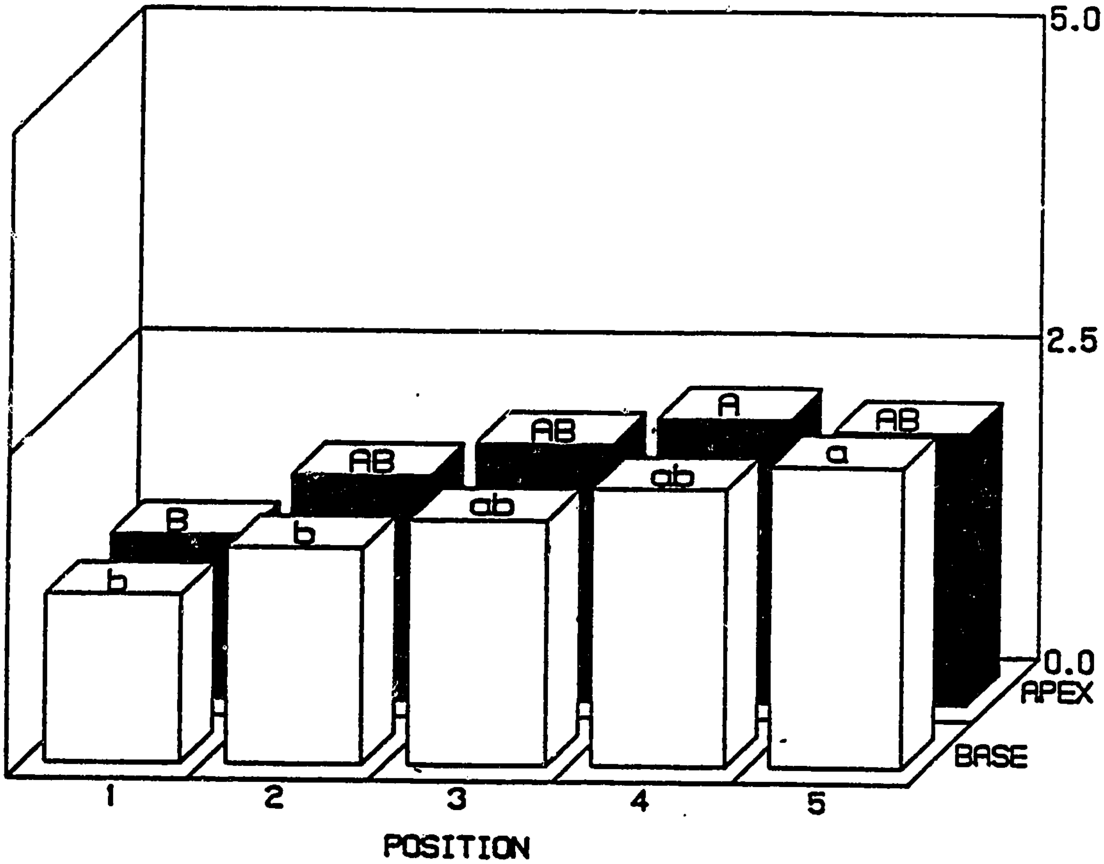


FIG. 3 - 3 DIAMETER OF NODAL SEGMENT PLOTTED AGAINST POSITION ON RHIZOME FOR PARENTAL BASE AND RHIZOME APEX SEGMENT TYPES. 1-way ANOVA conducted (Table 3-1) and multiple comparison of means (T-K method) done separately on each rhizome segment type. Similar letters within each segment type denote no significant difference.

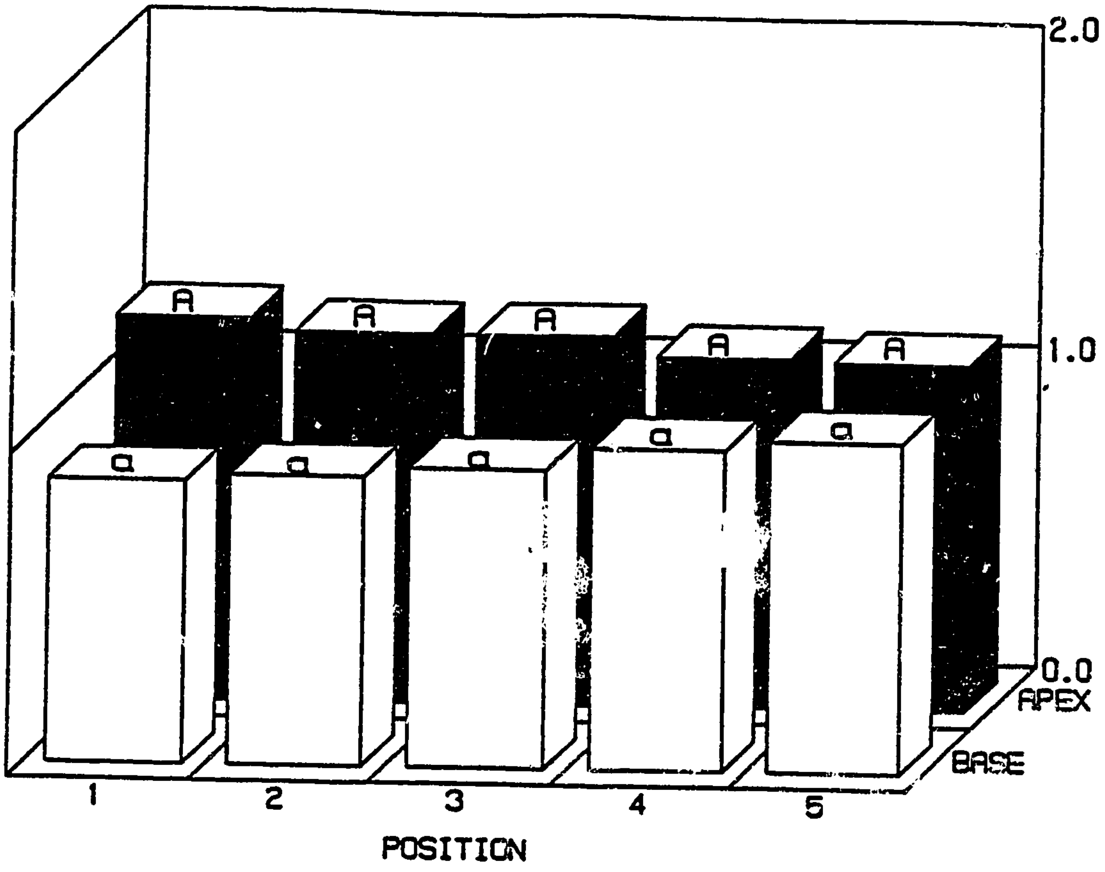


FIG. 3 - 4 WEIGHT OF NODAL SEGMENT PLOTTED AGAINST POSITION ON RHIZOME FOR PARENTAL BASE AND RHIZOME APEX SEGMENT TYPES. 1-way ANOVA conducted (Table 3-1) and multiple comparison of means (T-K method) done separately on each rhizome segment type. Similar letters within each segment type denote no significant difference.

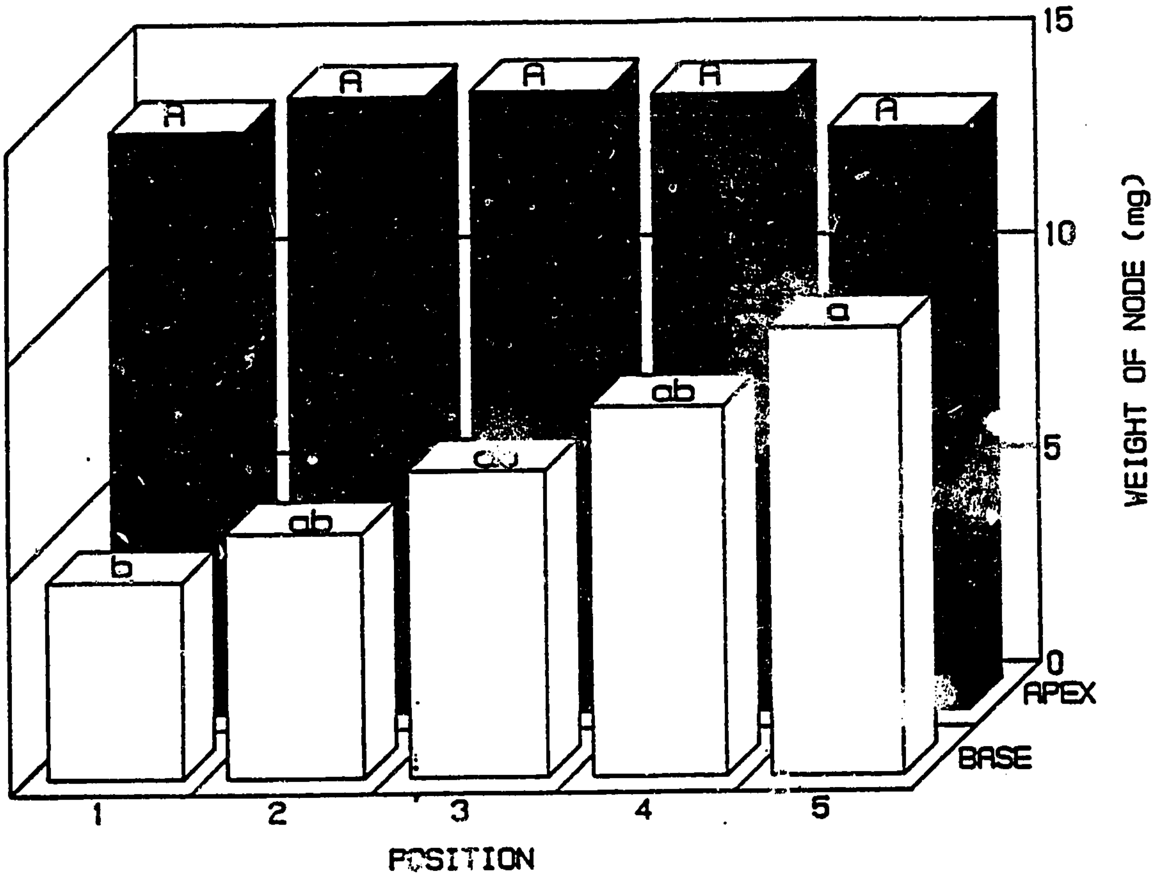


FIG. 3 - 5 TOTAL NON - STRUCTURAL CARBOHYDRATE CONTENT OF EACH NODAL SEGMENT STATED AS A PERCENTAGE OF TOTAL NODAL SEGMENT WEIGHT PLOTTED AGAINST POSITION ON RHIZOME FOR PARENTAL BASE AND RHIZOME APEX SEGMENT TYPES.
1-way ANOVA conducted (Table 3-1) and multiple comparison of means (T-K method) done separately on each rhizome segment type. Similar letters within each segment type denote no significant difference.

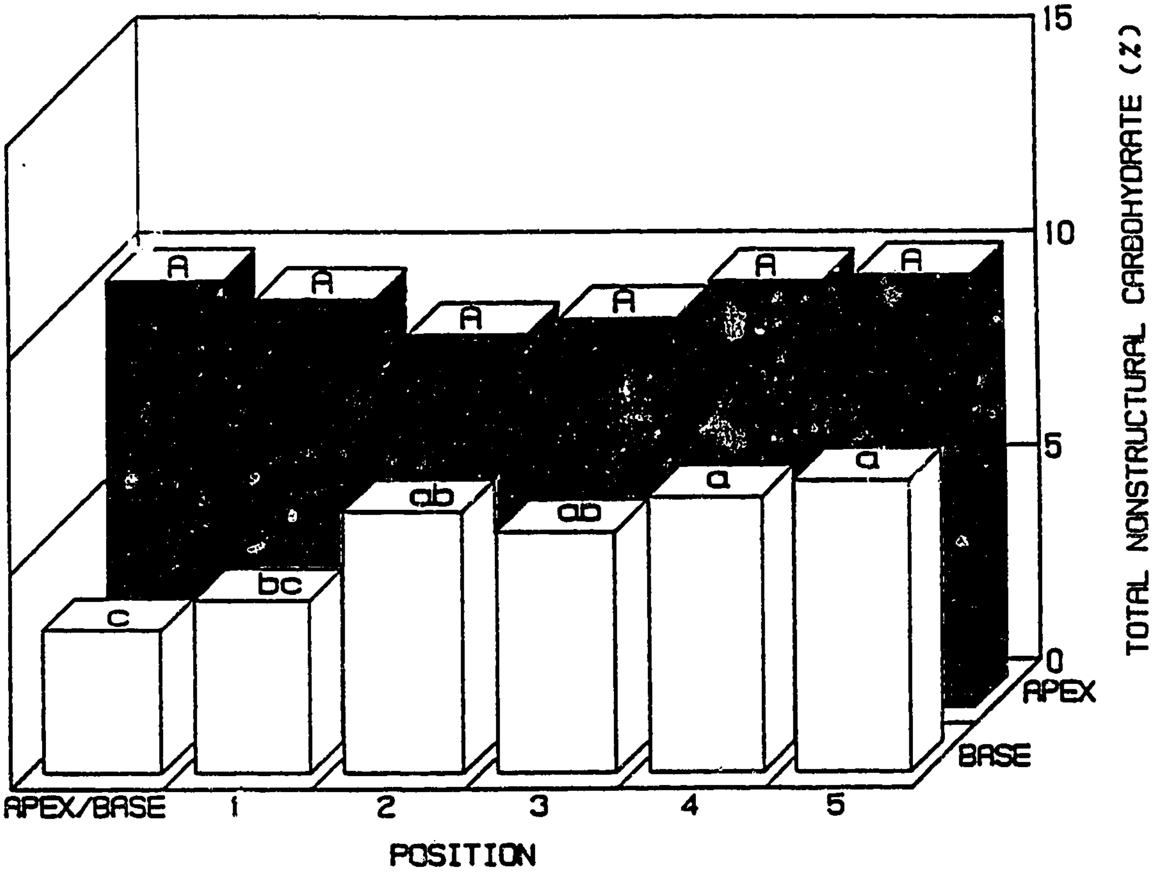


FIG. 3 - 6 FREQUENCY OF BUD DEVELOPMENT BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.
For statisitical analysis see Table 3-2 and Table 3-3.

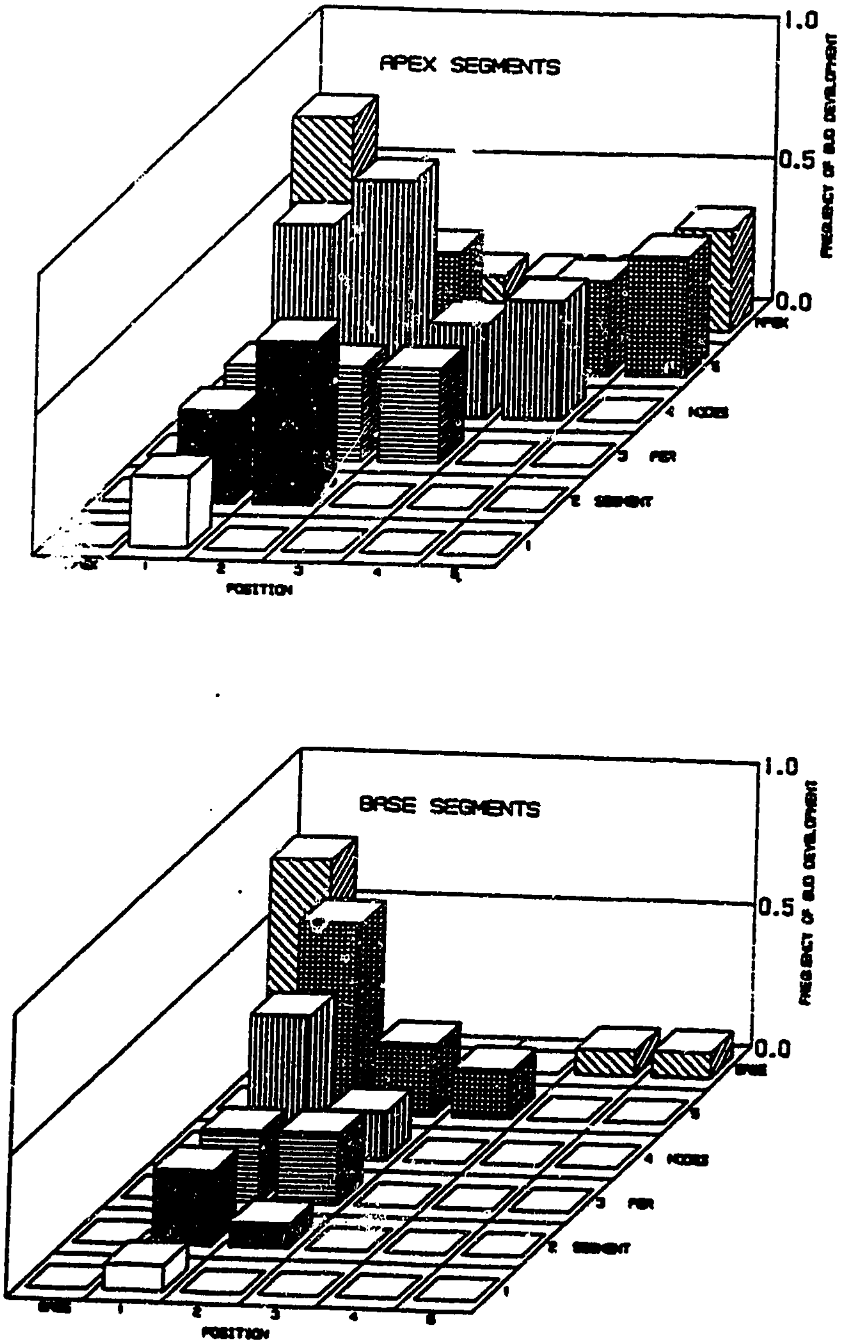
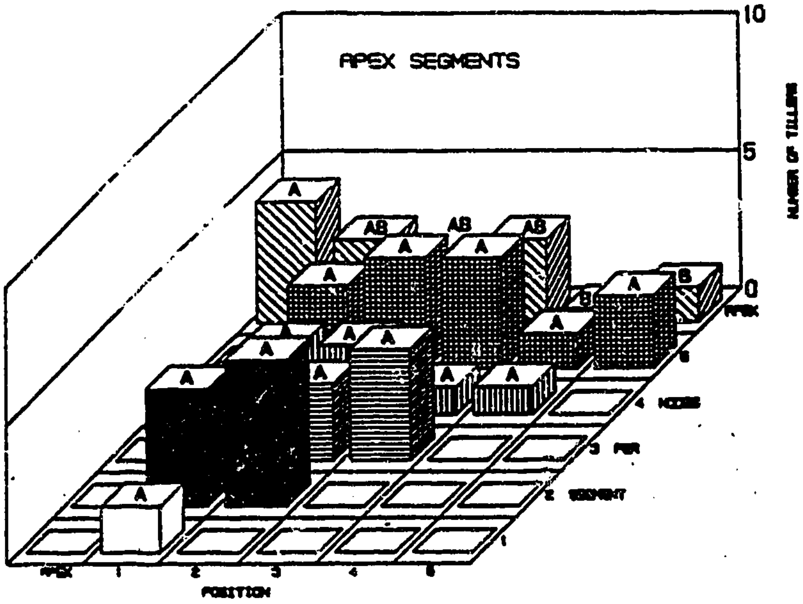


FIG. 3 - 7 NUMBER OF TILLERS PRODUCED FOR EACH DEVELOPED BUD BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.

1-way ANOVA and multiple comparison of means (T-K method) conducted on vertical columns (positions) and horizontal rows (nodes per segment). No significant differences were found in columns, thus only differences within rows are shown. Similar letters within rows designates no significant difference.



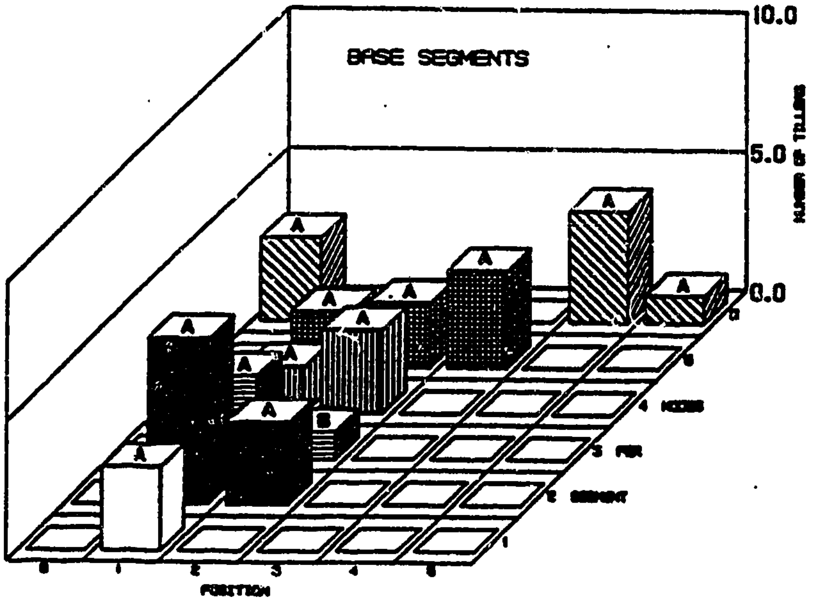


FIG. 3 - 8 TOTAL TILLER WEIGHT FOR EACH DEVELOPED BUD BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.
1-way ANOVA and multiple comparison of means (T-K method) conducted on vertical columns (positions) and horizontal rows (nodes per segment). No significant differences were found in columns, thus only differences within rows are shown. Similar letters within rows designates no significant difference.

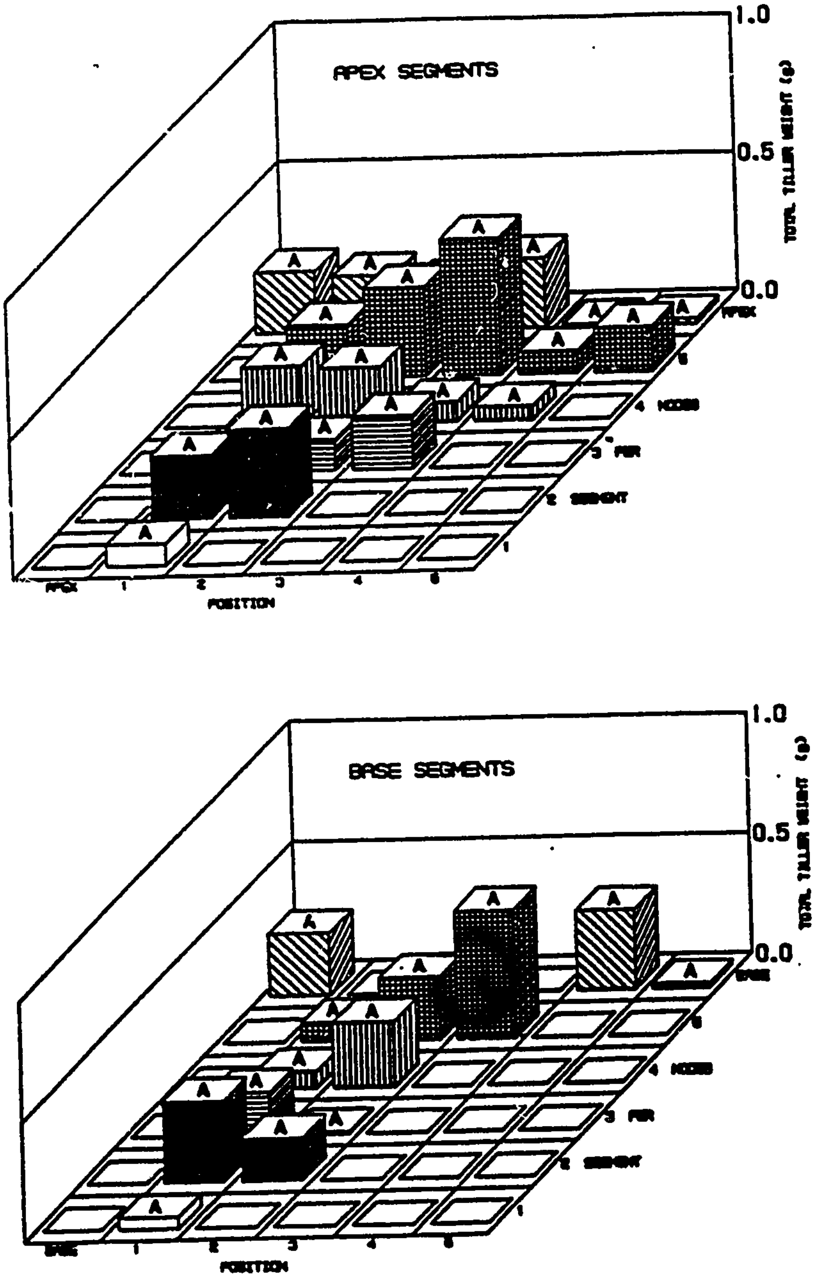


FIG. 3 - 9 NUMBER OF RHIZOMES PRODUCED FOR EACH DEVELOPED BUD BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.

1-way ANOVA and multiple comparison of means (T-K method) conducted on vertical columns (positions) and horizontal rows (nodes per segment). No significant differences were found in columns, thus only differences within rows are shown. Similar letters within rows designates no significant difference.

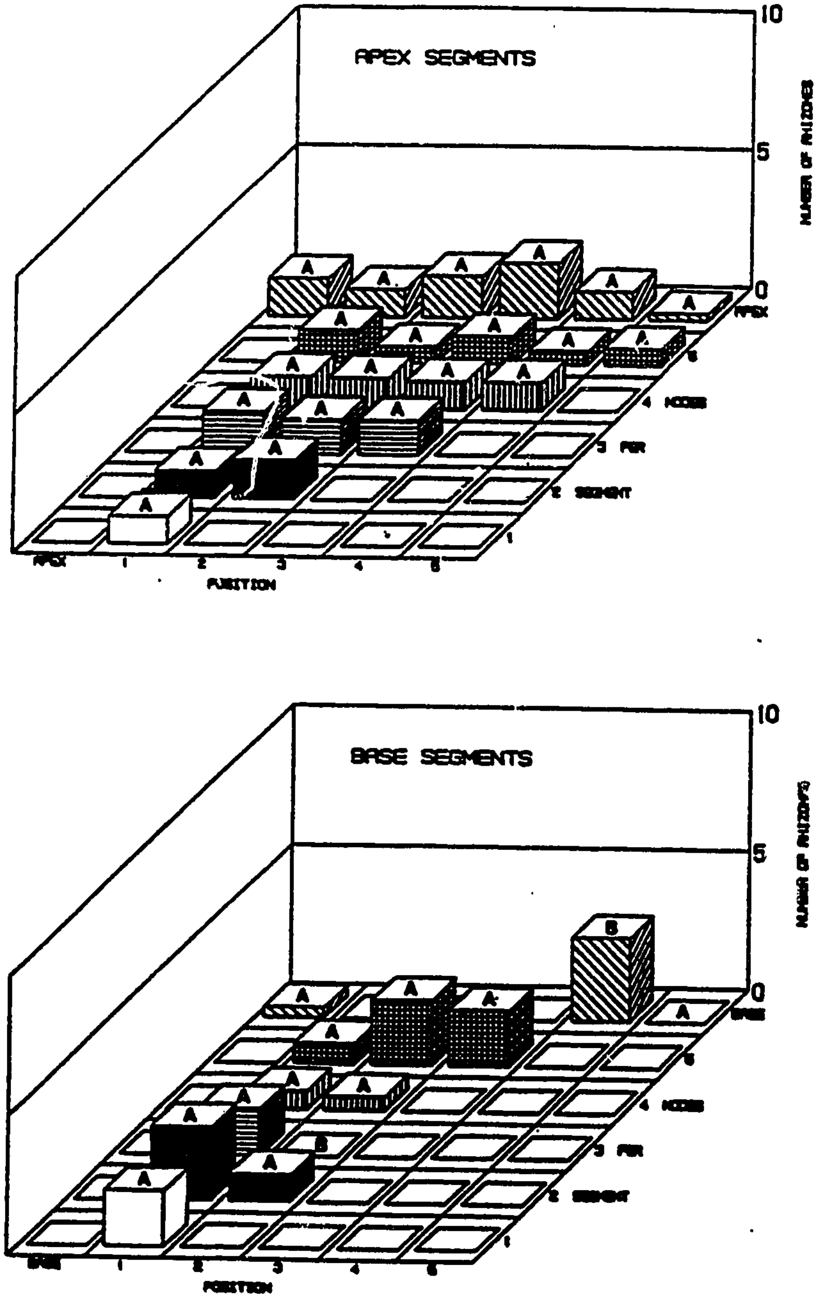


FIG. 3 - 10 RHIZOME WEIGHT FOR EACH DEVELOPED BUD BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.

1-way ANOVA and multiple comparison of means (T-K method) conducted on vertical columns (positions) and horizontal rows (nodes per segment). No significant differences were found in columns, thus only differences within rows are shown. Similar letters within rows designates no significant difference.

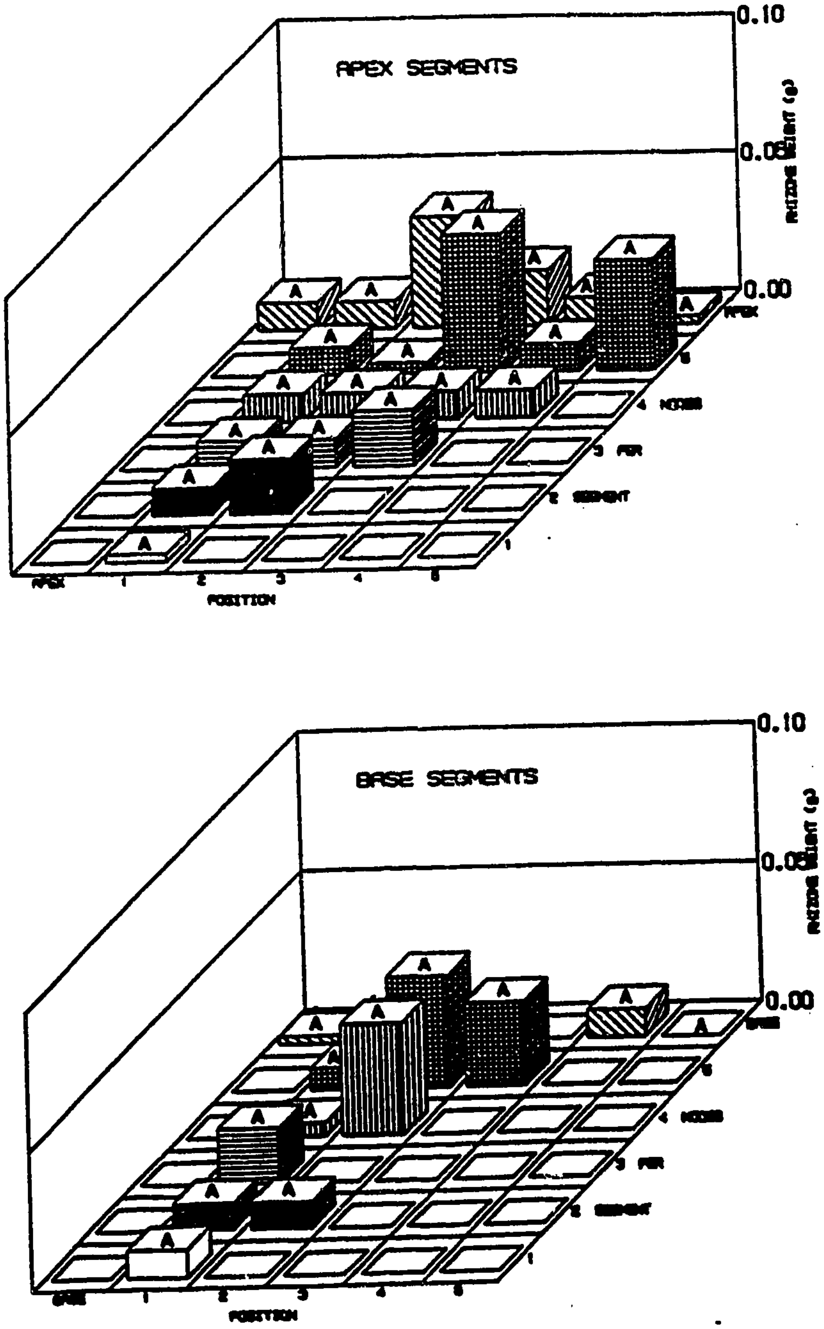
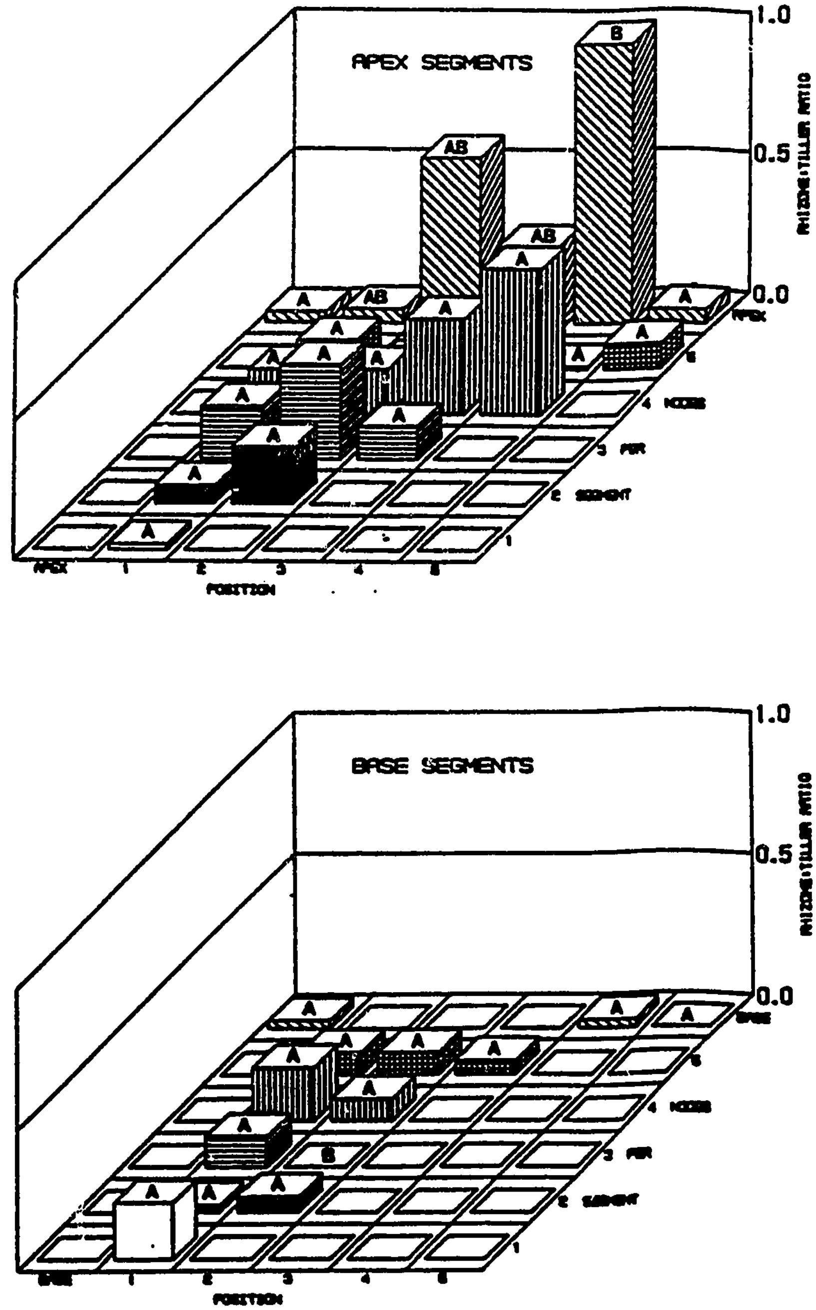


FIG. 3 - 11 RHIZOME:TILLER RATIO FOR EACH INITIATED BUD BY POSITION AND NUMBER OF NODES PER SEGMENT FOR RHIZOME APEX AND PARENTAL BASE SEGMENT TYPES.
1-way ANOVA and multiple comparison of means (T-K method) conducted on vertical columns (positions) and horizontal rows (nodes per segment). No significant differences were found in columns, thus only differences within rows are shown. Similar letters within rows designates no significant difference.



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CONCLUSION

CONCLUSION

If the management of cutblocks in areas of potentially high infestations of C. canadensis is to be successful, an understanding of this species' growth characteristics in response to different environmental conditions and disturbance is necessary. This series of studies has removed some misconceptions and shed some insight on the growth strategy of C. canadensis. These studies have determined that:

1) rhizome segments adjacent to the rhizome apex are thicker, heavier and have a higher non-structural carbohydrate content than segments adjacent to the parental base,

2) nodal length increases with distance from both the rhizome apex and parental base,

3) the more buds present on a severed rhizome segment (i.e. the longer the segment) adjacent to the apex with the apex excised, the higher the frequency of dormant bud development,

4) buds on severed rhizomes adjacent to the apex have a higher frequency of development, thus higher regenerative capacity, than buds on severed rhizomes adjacent to the parental base,

5) a priority of bud development which favours the bud closest to the parental base is established when the parent and apex are excised,

6) there is no priority of bud development on severed rhizome segments adjacent to the apex when it is excised,

7) development of the dormant buds may be dependent on the condition of the emergent environment, and not on the position or

carbohydrate status of the severed rhizome segment,

8) plant growth, including rhizome production, increases with light intensity and nutrient availability,

9) nutrient availability only alters plant growth when light intensity is at moderate and high levels,

10) proportional biomass allocation to rhizomes reaches a maximum under open canopy conditions,

and 11) in field conditions non-structural carbohydrate storage in rhizomes increases with light intensity.

When the findings of these two studies are combined and applied to forest management it could be assumed that soil disturbance and rhizome severing of C. canadensis will promote new grass plant establishment upon the site. However, rhizome production and total rhizome mass under low light conditions is small, thus, any soil disturbance following the harvest of a closed canopy stand will not promote much spread of C. canadensis by rhizome fragments. However, once the grass stand is well established, either under an open canopy forest or in the middle of a cutblock, further disturbance of the soil will facilitate the spread of C. canadensis by rhizome fragments.

It is under the reduced light levels of the forest canopy, however, that above ground biomasss production of C. canadensis is severly reduced. Under an open canopy forest, the light levels may be high enough to promote the growth of white spruce at an adaquate rate but light levels may be low enough to restrict the above ground biomass production by C. canadensis. The overstory canopy can then be used as a "nurse crop" to allow white spruce to acheive a height (>50 cm) that will overcome any competition by C. canadensis if the overstory canopy is removed at a later date.

After C. canadensis becomes established upon a forest cutblock the higher light levels and nutrient availablity increase the biomass production of this grass. Under these conditions, the grass plant will produce numerous tillers which will, presumably, decrease the amount of light reaching the soil surface, delay soil heating in the spring and prevent conifer seeds from reaching the soil surface. The large root biomass produced by C. canadensis under high light intensity and high nutrient availability may reduce the amount of soil moisture available to a conifer seedling growing on the site. Biomass allocation to the rhizomes on these sites will also be high. Presumably the higher biomass and non-structural carbohydrate content of each rhizome will translate into a higher regenerative capacity, making further soil disturbance inadvisable.

While some insights into the growth strategy of C. canadensis have been determined, important questions still remain. These include:

1) Do rhizomes from a clearcut/open site have a higher regenerative capacity than rhizomes from a reduced light environment?

2) How effective are different types of site preparation methods in reducing the spread of C. canadensis by rhizome fragments?

3) What are the physiological responses of C. canadensis to different light and nutrient regimes?

4) How does planting depth alter dormant bud response to severing

on C. *canadensis* rhizomes?

5) What are the endogenous growth regulators involved in the control of bud activity on C. *canadensis* rhizomes?

and 6) What is the phenology of C. *canadensis* in northern Alberta?