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Ecological Aspects Of Regeneration From Root Fragments In Two Physalis Species

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ECOLOGICAL ASPECTS OF REGENERATION FROM ROOT FRAGMENTS IN TWO *PHYSALIS* SPECIES

by

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of the requirements for the degree of
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ABSTRACT

Clammy (Physalis heterophylla Nees.) and smooth (P. virginiana Mill. var. subglabrata (Mackenz. and Bush) Waterfall) ground-cherry are perennial herbs that grow in cultivated fields, roadsides, pastures, and open woodlands. It was postulated that both species are capable of surviving in highly disturbed habitats because of their extensive root systems and their capacity to regenerate from root fragments. Field and greenhouse experiments were conducted in 1991 and 1992 to investigate the effects of root fragment size, depth of root burial, root fragment orientation at planting, plant growth stage at the time of root fragmentation, and origin of the root fragments, on their subsequent capacity to regenerate. The root systems of both species consisted of short feeding roots and long perennating roots. Only the long root type was capable of vegetative regeneration. Lateral long roots branched from the main vertical tap root two to ten cm below the soil surface. These lateral long roots grew horizontally before turning down at various distances from the main vertical tap root. Clammy ground-cherry produced more long roots and underground shoots than smooth ground-cherry.

Both species were capable of regenerating from root fragments as short as 2.5 cm and could send up shoots from at least a 15 cm soil depth. No root fragment survived at the soil surface. Orientation had no effect on the capacity of the two species to regenerate from root fragments. In both species significantly fewer fragments sampled from

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CHAPTER ONE

INTRODUCTION

1.1 Introduction

Vegetative regeneration is a term embracing lateral spread by creeping shoots, roots, etc. and the production of fragmented parts of plants (Leakey, 1981). The term vegetative reproduction is a controversial one. Some workers consider reproduction to be the result of sexual union of gametes only (Harper, 1977). On the other hand Urbanska (1990) emphasizes the need for considering reproduction as the process resulting in the formation of active offspring and not necessarily completed by the production of propagules alone. Urbanska (1990) defines reproduction as the biological process resulting in the formation of physiologically autonomous offspring individuals. In clonal plants, many clones become fragmented and their separated parts have independent fates (Cook, 1985; Urbanska, 1990).

Where both vegetative and sexual reproduction occur together, the vegetative offspring will develop immediately, and quickly become adults, usually with a larger food supply individually than that associated with seeds (Abrahamson, 1980). The potential for rapid adaptation is probably greater in species that reproduce by both sexual and vegetative means than in those relying on one type (Leakey, 1981; Kigel and Koller, 1985). Vegetative regeneration can maintain the continuity of a genotype adapted to a certain habitat whereas genetic recombination can lead to the breakdown of desirable traits (Kigel and Koller, 1985). The most consistent feature of vegetative expansion is the low risk of mortality to the offspring (Grime, 1979). In *Elytrigia repens* (L.) Nevski (Sarukhan, 1974), and *Trifolium repens* L. (Turkington et al. 1979) seedlings are less likely to become established than daughter plants connected to the parent plant. Hawthorn and Cavers (1976), working with *Plantago* spp., found that the probability of death is highest at the seedling and later juvenile stages. The most obvious drawbacks of vegetative regeneration are greater susceptibility to elimination by cultivation, less effective dispersal and a lack of genetic variation (Aldrich, 1984). Baker (1965) described vegetative regeneration as a characteristic of the ideal weed.

The vegetative propagation of many perennial dicotyledonous plants by the production of adventitious stems has been well documented (Raju et al. 1966). Some of these plants are serious weeds in agriculture because they persist in soils after the usual cultural practices for weed control. Roots of many species including *Convolvulus arvensis* L. (Bonnet and Torrey, 1965), *Euphorbia esula* L. (Raju et al. 1963), *Cirsium arvense* (L.) Scop. (Hamdoun, 1972); *Sonchus arvensis* L. (Lemna and Messersmith, 1990), and *Chondrilla juncea* L. (Cuthbertson, 1972) produce shoots from root buds. Regeneration from root buds is also important in some horticultural species, e.g. raspberries have been propagated from root pieces (Hudson, 1953). Raju et al. (1966) pointed out that some of the most persistent perennial weeds on the prairies have been able to survive adverse conditions partially through their capacity to regenerate from root buds. There is no doubt that perennial species capable of both vegetative regeneration and reproduction by seed can show rapid adaptation and tolerance to unfavourable conditions, compared to species using only one method of propagation.

Clammy (*Physalis heterophylla* Nees) and smooth (*P. virginiana* Mill. var. *subglabrata* (Mackenz. and Bush)) ground-cherry are perennial native herbs capable of reproducing from adventitious buds formed on their root systems. Preliminary greenhouse studies that I conducted in 1990 revealed that both species are self-incompatible. Agricultural researchers in southwestern Ontario describe these species as "problem weeds" because of their thick deep penetrating and extensive root sytems and their resistance to herbicides (R. Brown and J. Shaw, pers. comm.). As the herbaceous shoots of clammy and smooth ground-cherry do not survive the harsh winter conditions, their roots and root buds are essential for their perennation (Abdullahi, unpublished). The severity of infestations of these species can be predicted by studying the capacity of their root systems to spread and develop new shoots. The growing use of reduced or zero-tillage has increased the importance of herbicide use as a control measure (Aldrich, 1984). If root regeneration of ground-cherry species is as significant as suspected, it is then important that herbicides be translocated to the deep root systems of these species in order to make control effective.

Investigations on vegetatively regenerating species have concentrated on rhizomatous species, or in the case of regeneration from roots, observations were taken from already established stands, or the investigations were only conducted under greenhouse conditions (Raju et al 1964; Charlton, 1966; Hamdoun, 1972; Sosters and Murray, 1982). No previous study addressed the capacity of regeneration from root fragments under field conditions in perennial species living in cultivated cropland. Furthermore, no previous study compared the regenerative capacities from root segments in congeneric species. In addition, very little is known about the ecology of the two species of ground-cherry.

It was postulated that the two species are persistent in cultivated fields because of their ability to produce both extensive horizontal lateral roots and deep-penetrating vertical roots with buds; their capacity to regenerate from root fragments of different sizes; the capacity of their root fragments to resist decay and to overwinter; and their resistance to commonly used herbicides.

1.2 Objectives of the thesis

The objectives of this project were:

a) to describe the root systems of clammy and smooth ground-cherry under conditions prevalent in southwestern Ontario;

b) to investigate the factors that affect the capacity of the root system to develop shoots from root fragments under greenhouse and field conditions;

c) to study the response of smooth ground-cherry to different herbicides.

In order to facilitate publication of individual papers, the chapters of the thesis are written in a paper format.

CHAPTER TWO

LITERATURE REVIEW

2.1 Description

Smooth and clammy ground-cherry (Solanaceae) are perennial herbs propagating from root buds and reproducing by seeds (Abdullahi et al. 1991). The stems are much branched; erect to 1 m high and ridged, often with a greyish tint in smooth ground-cherry; spreading to erect, up to 70 cm high in clammy ground-cherry (Fig. 1). The leaves are arranged alternately on the stems; oval or lance shaped; with slightly toothed or entire margins in smooth ground-cherry and toothed margins in clammy ground-cherry (Fig. 1). Both the leaves and stems of clammy ground-cherry are covered with sticky hair giving a clammy texture. Smooth ground-cherry is sparsely hairy on stems and leaf margins. The flowers of both species are bell-shaped, drooping singly where three branches or leaves meet; yellow with a star-shaped dark purplish centre; and measure about 2.7 cm x 2.8 cm. Flower pedicels measure about 1.5 cm long and elongate to 2.5 cm after fruit formation. Flowering begins about six weeks after emergence, which occurs on the first to the second week of May, and continues up to September. The fruits are berries loosely enclosed by the much enlarged calyx and are 20, and 15 mm thick at maturity, in clammy and

Fig. 1. Plants of clammy (A) and smooth (B) ground-cherries (x 0.3). Note the abundant hair covering the leaves and stems of clammy ground-cherry, and the drooping, bell-shaped flower in smooth ground-cherry. Clammy ground-cherry has a similar flower. Adapted from Abdullahi et al. 1991.

smooth ground-cherry, respectively. Berries are green at first and red or yellow at maturity; and contain about 200 and 150 seeds in smooth ground-cherry and clammy ground-cherry, respectively (Fig. 2). The seeds are orange-coloured at maturity; measure 2.0 mm X 1.5 mm and 1.8 mm X 1.3 mm; and weigh 0.80 and 0.54 g per thousand in clammy ground-cherry and smooth ground-cherry respectively.

2.2 Distribution

P. virginiana var. *subglabrata* and *P. heterophylla* are native to Canada and the United States (Waterfall, 1958).

Clammy ground-cherry occurs in open woods, prairies, hillsides, fields, and disturbed habitats from Manitoba east to Ontario, Quebec (north to Ste-Anne-de-la-Pocatiere, Kamouraska County), and Nova Scotia (Kings County), south to Texas, Oklahoma and Georgia (Scoggan, 1979). In Ontario, clammy ground-cherry grows in open woods, old fields, cultivated fields, roadsides, and railway embankments (Abdullahi et al. 1991). It is usually found growing in light-textured sandy and gravelly soils.

Smooth ground-cherry occurs in woods, grasslands, roadsides, fields, and disturbed sites, from Manitoba (north to Makinak, about 130 km north of Brandon and Victoria Beach, about 88 km northeast of Winnipeg) east to Ontario (up to the Ottawa district), to southwest Quebec (the Montreal district), and south to New Mexico, Texas, Alabama and Georgia (Scoggan, 1979). In Ontario, smooth ground-

Fig. 2. (A): Four calyces of clammy ground-cherry, each enclosing one berry (x 1.0). (B): Berries of clammy ground-cherry ranging from freshly ripe and smooth to older and wrinkled (x 1.0). (Adapted from Abdullahi et al. 1991).

cherry grows in cropland, old fields and pastures; mostly in heavier textured soils than those of clammy ground-cherry (Abdullahi et al. 1991).

2.3 Biology

2.3.1 Taxonomy and genetics

Physalis is an American genus of about 100 species (Gleason, 1963), with funnel-shaped drooping flowers and an enlarged fruiting calyx that encloses the berry. In 1958 Waterfall carried out a detailed taxonomic study of the *Physalis* species of North America, north of Mexico. Menzel (1951) found that the haploid chromosome number of both smooth and clammy ground-cherry is 12. Menzel also showed experimentally that genetic isolation barriers are incomplete between some *Physalis* species. She obtained fertile hybrids between *Physalis viscosa* and *P. mollis* (Menzel, 1951), and between *P. viscosa* and *P. angustifolia* (Menzel, 1957).

Stober (1985) investigated the karyotypes of *P. heterophylla* and *P. virginiana* var. *subglabrata* and found that chromosome number 12 in *P. virginiana* var. *subglabrata* is quite distinct from the same numbered chromosome in *P. heterophylla* . In the former, the entire short arm is threadlike and terminated by a small knob or satellite, while in the latter an acrocentric chromosome with a distinct satellite is present. The average total length of the haploid chromosomal set in *P. virginiana* var.

subglabrata is significantly greater than that of P. heterophylla (Stober, 1985). These differences suggest that meiotic irregularities could be expected during microsporogenesis in hybrid plants. Hinton (1975) examined the possibility of hybridization between P. virginiana and P. heterophylla. Artificial hybridizations between these two species resulted in enlargement of the calyx and failure of the ovary to drop off in most cases, indicating successful pollination; but after all but one of these pollinations there was no enlargement of the ovary and no seed set. These pollination experiments indicated that a strong, but not absolute, isolation mechanism of noncrossability and hybrid sterility exists between P. virginiana and P. heterophylla.

2.3.2 Seed germination

In seed germination experiments conducted by Thomson and Witt (1987) P. virginiana var. subglabrata seeds failed to germinate in light or dark at constant temperatures of 5, 10, or 20° C, and very few seeds germinated at alternating temperatures of 10/20 C. The most complete and rapid germination occurred under an alternating temperature regime of 10/30 C (in the light) or under alternating temperatures of 10/30 or 20/30 C in the dark. Seeds of P. virginiana var. subglabrata became viable between 2 and 4 weeks after anthesis (Thomson and Witt, 1987).

2.4 Uses of *Physalis* spp.

Some members of the genus *Physalis* are cultivated as vegetable crops or are grown as ornamentals. Information in this paragraph comes mainly from Thomas (1981). The Chinese lantern plant (*P. alkekengi* L)., native from southeast Europe to Japan, earns its common name because of the handsome ribbed, orange-scarlet to scarlet calyces of its flowers. The stems, cut with the calyces attached and dried, make long-lasting decorations. The cape-gooseberry (*P. peruviana* L.), native of tropical South America, is cultivated for its edible yellow fruits. The husk-tomato (*P. pruinosa* L.) native from Massachusetts to Ontario, Iowa, Florida, and Tennessee, is grown for its edible fruits, which are sweeter than those of *P. peruviana* . The tomatillo (*P. ixocarpa* Brotero), is a horticultural crop that has been cultivated in Mexico since pre-Columbian times(Ramirez and Ochoa, 1991). Its fruits, known in Mexico as "tomato verde" (green tomato) or "tomate de cascara" (husk tomato) are used to prepare a green, savoury sauce. In Mexico, this crop occupies approximately 15,000 hectares and yields 160,000 tons per year (Ramirez and Ochoa, 1991). The fruits of tomatillo can be stored for several months in a cool, well-ventilated place, spread only one layer deep.

2.5 Smooth and clammy ground-cherries as weeds

During the last few years smooth and clammy ground-cherry have been increasing in importance as weeds of cultivated land in Ontario. In Southwestern Ontario new shoots arise from overwintered root systems in mid-May and continue emerging until late June (Abdullahi et al. 1991). Through the initiation of daughter colonies, single plants are capable of covering patches six metres wide in the field within two years. Tillage operations can spread these weeds into uninfested fields. Alex (1964) reported that Abutilon theophrasti Medic. Euphorbia maculata L., Apocynum cannabinum L., Physalis virginiana var. subglabrata, and Hibiscus trionum L. were important weeds in corn and tomato fields in Kent and Essex Counties (Ontario).

For a soybean field to be certified, Kentucky seed certification standards require that no more than 62 ground-cherry plants per hectare be present at inspection;and no seed of ground-cherry is allowed in a seed lot (Thomson and Witt, 1987). The berries are often crushed during harvest, causing the weed seeds to cling to the soybean seeds, or the berries pass through the combine screens and become a contaminant that is difficult to separate by means of conventional seed cleaning equipment (Thomson and Witt, 1987). Burnside and Wicks (1982) observed that in corn planted into untilled winter wheat stubble, the more difficult to control weed species were Abutilon theophrasti, Panicum dicotomiflorum Michx., Digitaria sanguinalis L., and Physalis heterophylla. At least some ground-cherry species contain the steroidal type (solanidine) of alkaloid found in other nightshade species (Blackwell, 1990). In ground-cherries, as in nightshades, the unripe fruit is considered more dangerous than the ripe fruit.

Heliothis virescens F. (Lepidoptera) a tobacco pest, was commonly found on *Physalis heterophylla* and on weedy populations of *Physalis subglabrata* Mack. and Bush (Sitchawat and Thurston, 1980). Nutter and Kuhn (1989) reported that *Physalis angulata* L. and *P. virginiana* Mill. were among the weed hosts of the tobacco etch virus.

In Southwestern Ontario the Colorado potato beetle ((*Leptinotarsa decemlineata* Say) (Coleoptera)) was found feeding on both clammy and smooth ground-cherry, but more intensively on the former (Abdullahi, unpublished). A less damaging insect, found grazing more on the leaves of smooth ground-cherry than on those of clammy ground-cherry, is the three-lined potato beetle (*Lemma trilineata* Olivier). The tobacco and tomato hornworms ((*Manduca sexta* L.; and *M. quinquemaculata* Haworth) (Lepidoptera)) were observed feeding on clammy ground-cherry grown at Environmental Sciences Western, the University of Western Ontario Field Station (near London, Ontario), in September of 1990 and 1992 but not on naturally occurring populations of clammy ground-cherry.

CHAPTER THREE

GROWTH AND DEVELOPMENT

3.1 Introduction

The ability of many perennial plants to regenerate vegetatively from buds developed on the root system has been described in the botanical literature. The root system of some species will only regenerate after the root system has been damaged, e.g *Taraxacum officinale* Weber (Mann and Cavers, 1979); whereas others have the capacity to regenerate from buds located on intact root systems, e.g *Euphorbia esula* L. (Raju et al. 1964), and *Chondrilla juncea* L. (Cuthbertson, 1972).

The study of a root system poses a problem in that, unlike the shoot, it cannot be observed in its three-dimensional state without excavation; and the changes that it undergoes during its development cannot be observed as easily as in shoot growth (Raju and Steeves, 1964).

Clammy and smooth ground-cherry are capable of regenerating from the root system, as well as reproducing from seeds (Abdullahi et al. 1991). However, it seems that seeds are much less important than the root system in forming new stands of either species, at least under agricultural situations. The first report of the capacity of some *Physalis* species to regenerate from root buds was published by Holm (1925).

Studies on the regeneration and pattern of root growth from root fragments in perennial herbs has been very limited. Most previous studies examined root growth patterns in already established stands with root systems at least a few years old (Raju et al 1963; Charlton, 1966; Sosters and Murray, 1982). In other cases, only seedlings were used to study root growth patterns (Frazier, 1943 and 1944); or the investigations were carried out in the greenhouse (Hamdoun, 1972; Nadeau and Vanden Born, 1989). In addition to this, in very few investigations were comparisons made between plants regenerating from root fragments and plants establishing from seedlings.

It is widely accepted that interactions among plants, even at the early stages of growth and development, may have a direct influence on their subsequent biomass productivity (Ross and Harper, 1972). It is, therefore, important to study the phenology in general, and early patterns of root growth and extension in particular, of clammy and smooth ground-cherry to make meaningful comparisons between them and to derive conclusions about their capacity to regenerate from root fragments. Plant strategies for survival, both among and within species, include biomass allocation patterns and also differential phenology and growth (Harper and Ogden, 1970). On the other hand, an understanding of the phenology of a weed is important for formulating control measures (Leif and Oelke, 1990).

Field studies were conducted in 1992 to describe the patterns of root growth and overall plant development, both from root fragments and from seedlings in clammy and smooth ground-cherry. Further observations obtained in 1990 and 1991 from ground-cherry plants growing in cultivated fields, along roadsides and in abandoned fields were used as supplemental information on the two species.

In this chapter, root buds will refer to buds giving rise to shoots. Underground shoots will refer to shoots equal to or greater than 1 cm in length developing from roots or
below ground stem portions.

The objectives of this chapter were:

a) to describe the patterns of seasonal growth of clammy and smooth ground-cherry from root fragments, and from seedlings, under natural field conditions,

b) to characterize differences in growth between the two species and between plants originating from root fragments and those originating from seedlings.

3.2 Materials and Methods

3.2.1 Nature of below ground systems: Samples were obtained from the below ground parts of clammy and smooth ground-cherry plants at the flowering stage grown at Environmental Sciences Western. Ten micron cross sections were taken with a microtome (Reichert- Jung 2040, Germany). The sections were processed by means of the usual techniques (Sass, 1958) and stained with toluidine blue. These were then examined under the light microscope to see whether they were root or stem tissue. The sections were then photographed. To determine the transition zone, sections were taken just below the cotyledons down to 15 cm along the hypocotyl-root axis from clammy and smooth ground-cherry plants at flower bud initiation.

3.2.2 Seasonal growth: Roots of smooth and clammy ground-cherry were harvested in September 1991 from Mr. Jim Shaw's farm at Ridgetown, Ontario (42° 26′ N, 81° 54′ W) and from a field in Iona Station, Ontario (42° 43′, 81° 54′ W). The roots were taken to the greenhouse, and cleaned with tap water. They were then cut into 10-cm-long pieces with diameters ranging from 3 to 8 mm. These pieces were then planted at 5 cm depth in 20-cm-wide pots filled with greenhouse potting soil (black muck, coarse sand, peat moss, in proportions of 1:1:3) to 18 cm depth. The pots were watered twice daily, and received a weekly fertlizer solution of NPK (20:20:20) that also contained chelated trace elements: iron, 0.1%; manganese, 0.05%; zinc, 0.05%; boron, 0.05%; and copper, 0.02% (from McRitchie Distributing, Strathroy, Ontario).

On May 22 and 23, 1992 roots were harvested from these plants. The roots were washed with tap water, cut into 10-cm-long fragments 5 to 8 mm thick and planted in field plots at Environmental Sciences Western. The proximal end of each fragment was marked by an angular cut before planting. They were then planted 7 cm deep in rows 8 m long and 0.75 m wide with 0.5 m spacing between root fragments.

On May 16, 1992 clammy and smooth ground-cherry seeds were placed in petri dishes on top of filter paper and kept in an incubator at alternating temperatures of 20 - 35 C° and a 14 h photoperiod at the higher temperature. These seeds were obtained in September, 1991, from the two fields mentioned above (Ridgetown and Iona Station). At cotyledon emergence, the seedlings were transplanted into 12.5-cm-wide pots filled with greenhouse potting soil and fertilized weekly as described for the root fragments. Observations on growth parameters lateral root emergence were taken on the seedlings in petri dishes and while they were still in the greenhouse by excavating five randomly selected seedlings every two days. Seedlings of both species were transplanted on June 23, 1992, at the third-leaf stage, into the same field where the root fragments had been planted. Seedlings were planted at the same spacing as the root fragments. The experimental design used was a randomized complete block with five blocks. Root fragments and seedlings were randomly assigned to the four rows in each block. Notes on dates of shoot emergence were taken.

Starting on June 29, 1992 five plants originating from root fragments and five plants originating from seedlings were harvested weekly for each species until August 10, and then every two or three weeks until October 14, 1992 at which time the samplings were terminated. Plants were selected randomly from each block, and each plant represented a replication. In each harvest the roots were excavated with a fork and washed with tap water to remove soil. The total length of thick roots (thicker than 1.5 mm), and the number of below ground shoots were recorded. The patterns of lateral root and adventitious shoot bud emergence were noted. Plant height was measured from the base of the plant at soil level to the growing point of the tallest shoot. Leaf areas were measured with a leaf area meter with a conveyor belt assembly (LI-COR 3100, LI-COR, Inc., Lincoln, Nebraska). To determine dry weights, roots and shoots were separated at ground-level, and were then packed in paper bags and dried in an oven at 60° C until constant weight was achieved.

The data were analysed as a three-way Anova with species, origin (root or seedling), and harvest date as the factors (Steel and Torrie, 1980). The general linear models (SAS, 1990) was used to carry out the analysis of variance. Results are reported on a per plant basis.

In the summers of 1990 and 1991, additional information on root growth patterns was obtained through supplemental obervations made by excavating the root systems of clammy and smooth ground-cherries growing in cultivated fields and roadsides in Kent County, Ontario. The root systems were excavated during frequent field trips (at least one trip every three weeks). Following excavation up to 1 m depth the extent and pattern of root spread were noted. Information resulting from these observations is incorporated in this chapter.

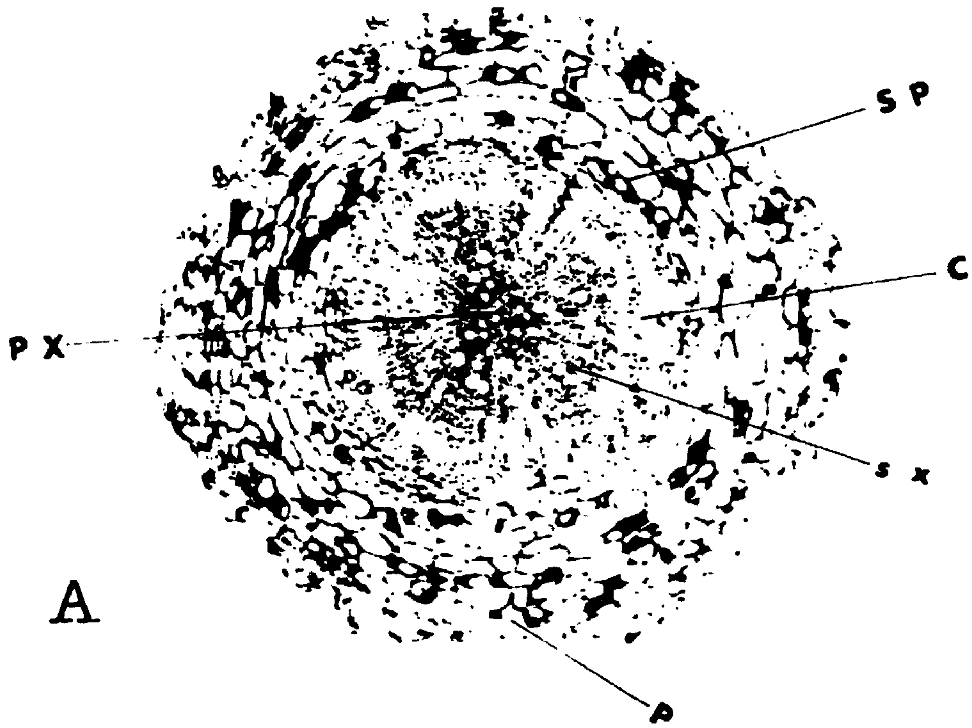
3.3 Results

3.3.1 Nature of below ground systems: The cross section of a root with secondary growth shows the ordinary layers of dicot roots. The roots at this stage were 4 to 6 mm thick (Fig. 3). A periderm has developed, and a central stele can be clearly seen. The sections do not show the presence of a central pith. In younger roots of both species xylem is arranged as triarch or tetrarch.

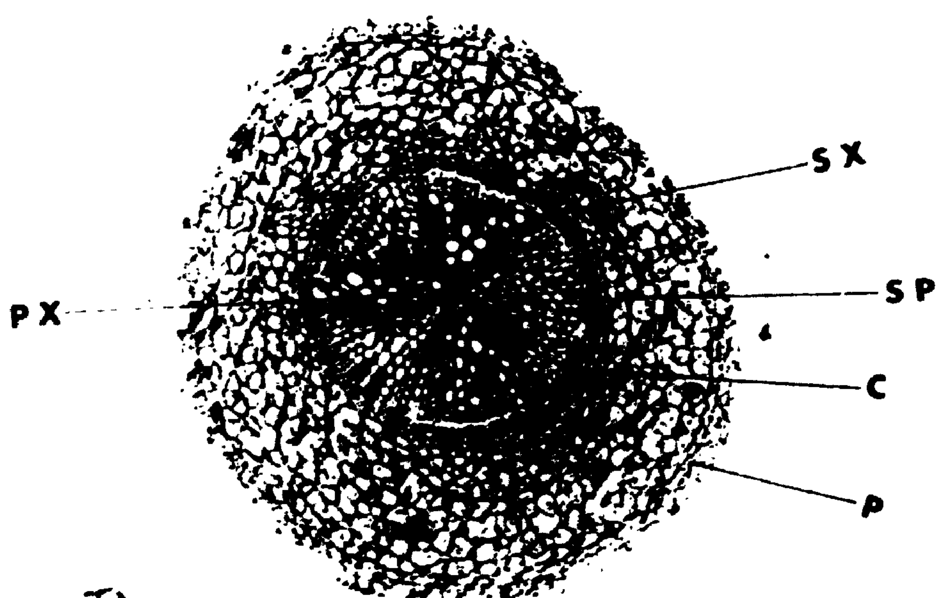
3.3.2 Root growth

Shoots emerged from most of the root fragments within four weeks of planting. The earliest shoots were visible above the soil surface three weeks after planting. Shoots mostly emerged from the proximal end (closer to the shoot) and roots from the distal end of root fragments, in both species. However, I noted that in some root fragments shoots and roots could develop from any location along the root length (Fig. 4). Lateral roots branched from the main tap root 2 to 10 cm below the soil surface. In many instances vertical and lateral roots developed from the underground stem of emerging shoots. In several cases roots and shoots emerged from sites about 2 mm apart within the same root fragment.

Fig. 3. Cross section of roots of smooth ground-cherry (A) X 70, and clammy ground-cherry (B) x 50. SX secondary xylem, PX primary xylem, SP secondary phloem, C cambium, P periderm.



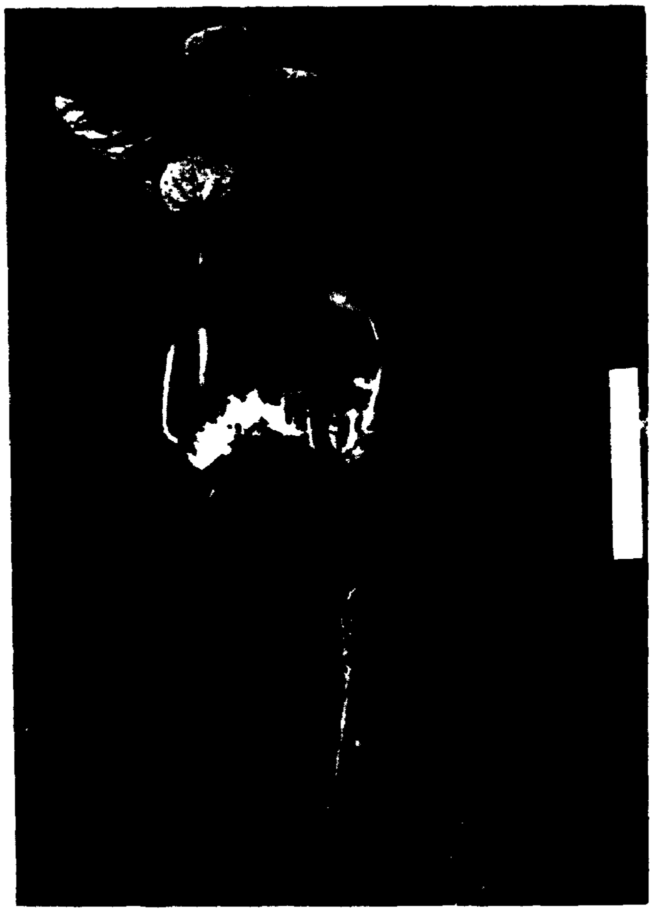
A



B

Fig. 4. Shoots and new roots emergent from root fragments of smooth (A) and clammy (B) ground-cherries five weeks after planting in field plots. The inset is of 5 cm length. Note the roots emergent from the vertical underground shoots.

A



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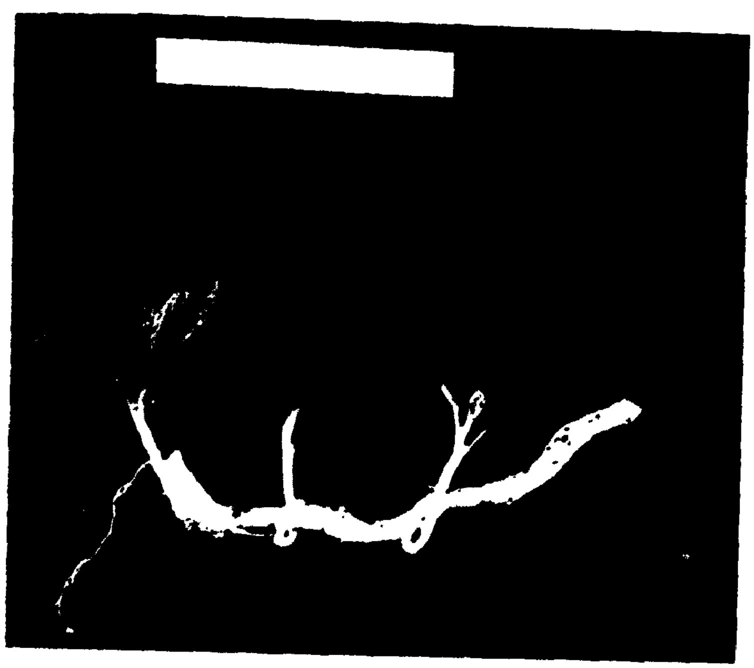
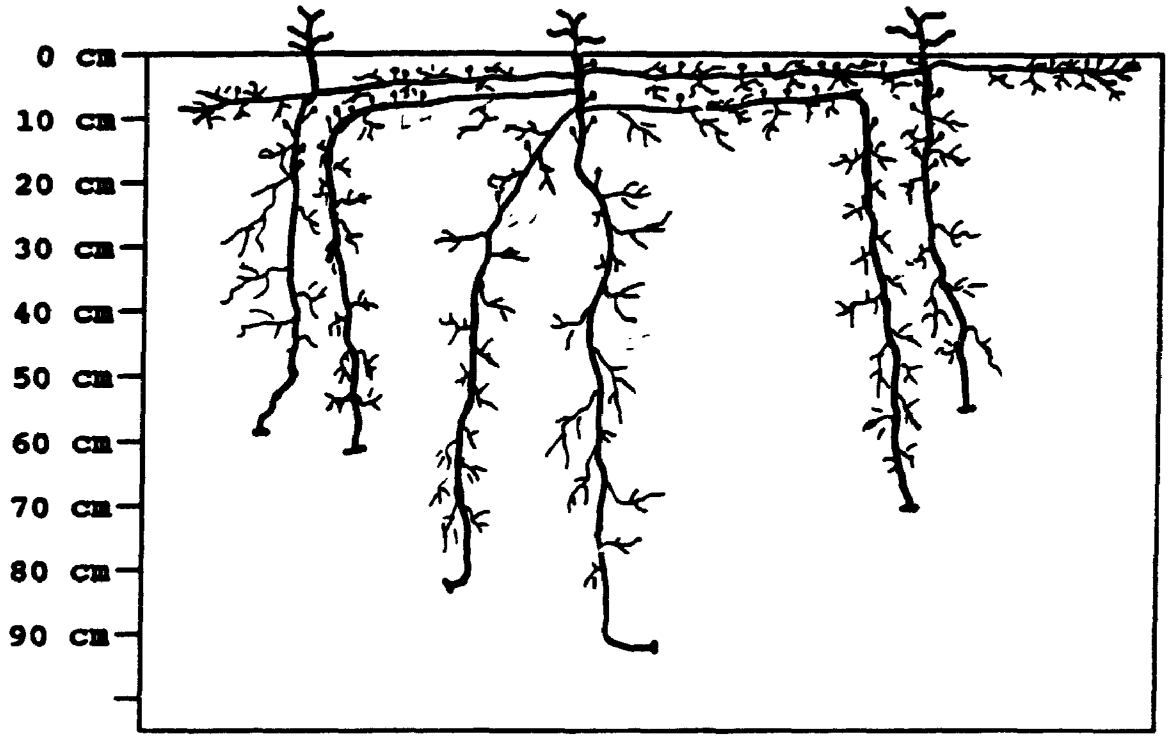


Seeds germinated within a week of incubation, with smooth ground-cherry seeds germinating slightly faster than those of clammy ground-cherry. The radicle emerged first, followed by the embryonic shoot. The first lateral roots were produced in seedlings at the time of initiation of the first true leaf, about two weeks after cotyledon emergence. In both species, the transition zone is about 3 to 5 cm below the cotyledons. In most seedlings of both species lateral roots also developed from the hypoctyl. As in root fragments, lateral roots branched from the vertical tap root at just below the soil surface to 10 cm deep. In both seed-originating and root-originating plants secondary laterals were being formed on the first order laterals as more first order laterals were being formed in acropetal succession behind the apex of the main vertical root. In both root-derived and seed-derived plants some of the lateral roots assumed horizontal growth while some grew in a vertical direction.

Adventitious shoot buds were visible in seedlings at five weeks after planting; and eight and nine weeks after planting in plants originating from root fragments, for clammy and smooth ground-cherry, respectively. These buds mainly emerged from the thicker part of the tap root in regions close to the soil surface. As plant growth progressed buds also developed on lateral horizontal roots and on deeper portions of the vertical root. In both seed-derived and root-derived plants buds were generally visible on roots about 1.5 mm thick or thicker. In root-derived plants shoot buds and new roots were also emerging from the underground stem portions (Figs. 4 & 5).

The root system both in plants originating from seed and those originating from root fragments, included a fine network of short feeding roots (Figs. 4 & 5). The root systems continued to spread laterally and to penetrate deeper into the soil, while at the same time increasing in diameter. In roots of both species excavated from crop fields in Ridgetown, root depth continued beyond a meter. In both species, regardless of origin, some horizontal laterals turned down to make positive geotropic growth after elongating to 15 to 50 cm in horizontal spread from the main vertical root (Fig. 5). In their horizontal growth these lateral roots became increased in thickness as they approached the vertical turning point (Fig. 5). At the turning point and below it these roots became even thicker. New horizontal laterals were formed at the turning point to continue the horizontal spread. There were more shoot buds at the bending point compared to the preceding portion of the root system. Many of these buds later became below ground shoots and in some cases emerged above the soil surface to become secondary shoots. Overall, there were many more shoot buds on horizontal laterals closer to the soil surface than on deep vertical roots. However, portions of the main vertical root close to the soil surface also had as many shoot buds. In both species, irrespective of origin,

Fig. 5. Pattern of root growth in clammy (A) and smooth (B) ground-cherry 16 weeks after planting in field plots. Note the increase in thickness at the turning point of the horizontal long roots. Projections ending with a knob are underground shoots. Termination of a root with a cross indicates that the root was still going deeper. LH = lateral horizontal root, LV = lateral vertical root, PT = primary tap root.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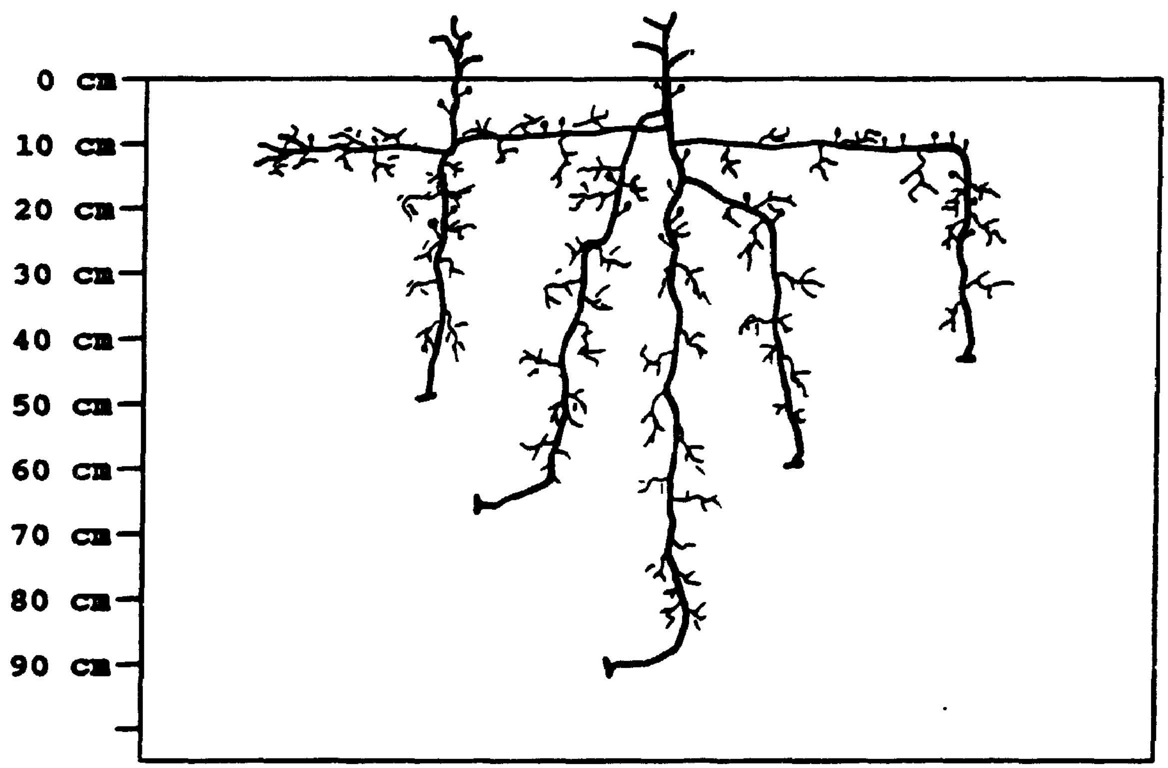
80 cm
90 cm

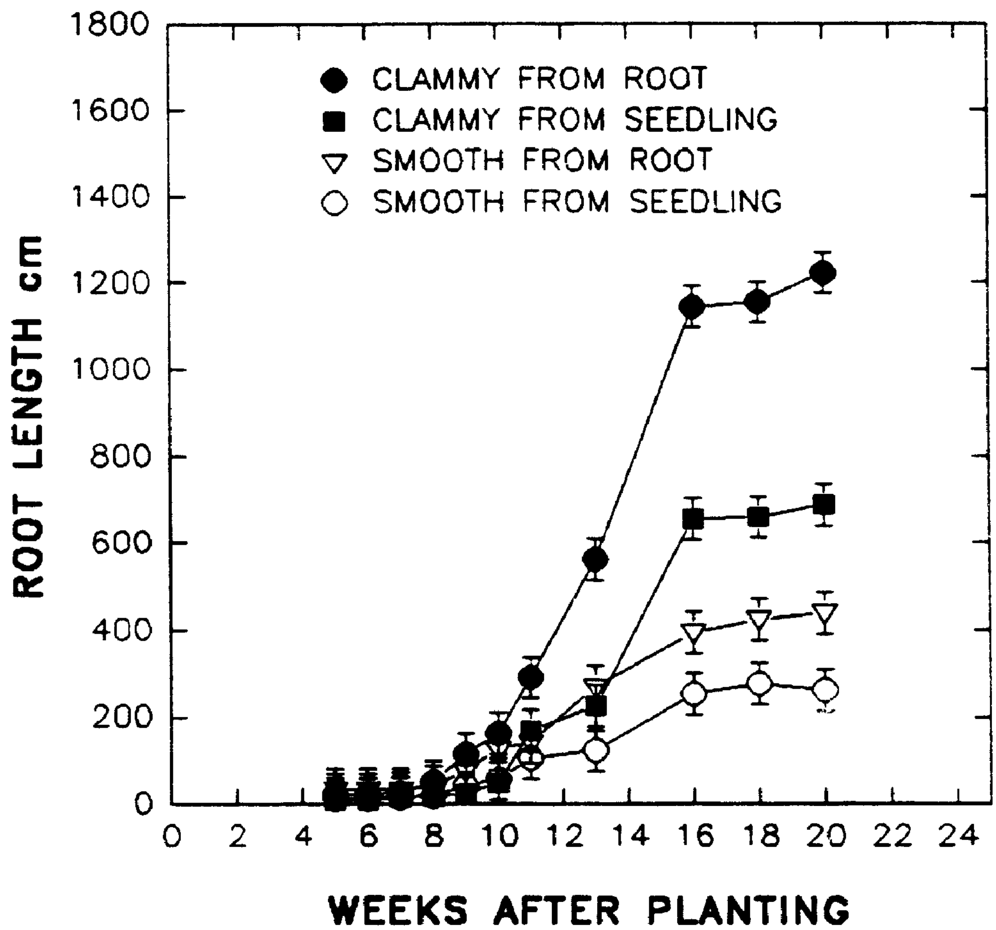

0 cm
10 cm
20 cm
30 cm
40 cm
50 cm
60 cm
70 cm
80 cm
90 cm

some thick horizontal roots never turned down. Plants of smooth ground-cherry had deeper penetrating vertical roots and fewer horizontal laterals than those of clammy ground-cherry.

In both species, long horizontal laterals had no visible buds along portions of their length closer to the main vertical taproot (i.e. closer to the main shoot). This region was generally thinner than portions further away from the main vertical root and was about 30 cm long by 16 weeks after planting. Long horizontal laterals 7 cm or less from the soil surface had no branches in either species. Similarly, there were no branches in vertical long roots at depths greater than 40 cm. Underground shoots were present in root-derived clammy ground-cherry and root-derived smooth ground-cherry, nine and ten weeks after planting, respectively, and in seed- derived plants eight weeks after planting.

The Anova results for this study are summarized in Appendix 1. Lengths of thick roots increased with time after planting in both species (Fig. 6). When data were averaged over all harvesting dates, clammy ground-cherry produced significantly ($p<0.001$) longer thick roots than those of smooth ground-cherry, irrespective of origin (Fig. 6 and Appendix 1). When data were averaged over both species and all harvest dates, long root length in plants originating from root fragments was twice that of plants from seedlings. Thick root length differences between species

Fig. 6. Average long root length (± S.E) of clammy and smooth ground-cherry established from root fragments and seedlings in field plots during 1992 growing season.



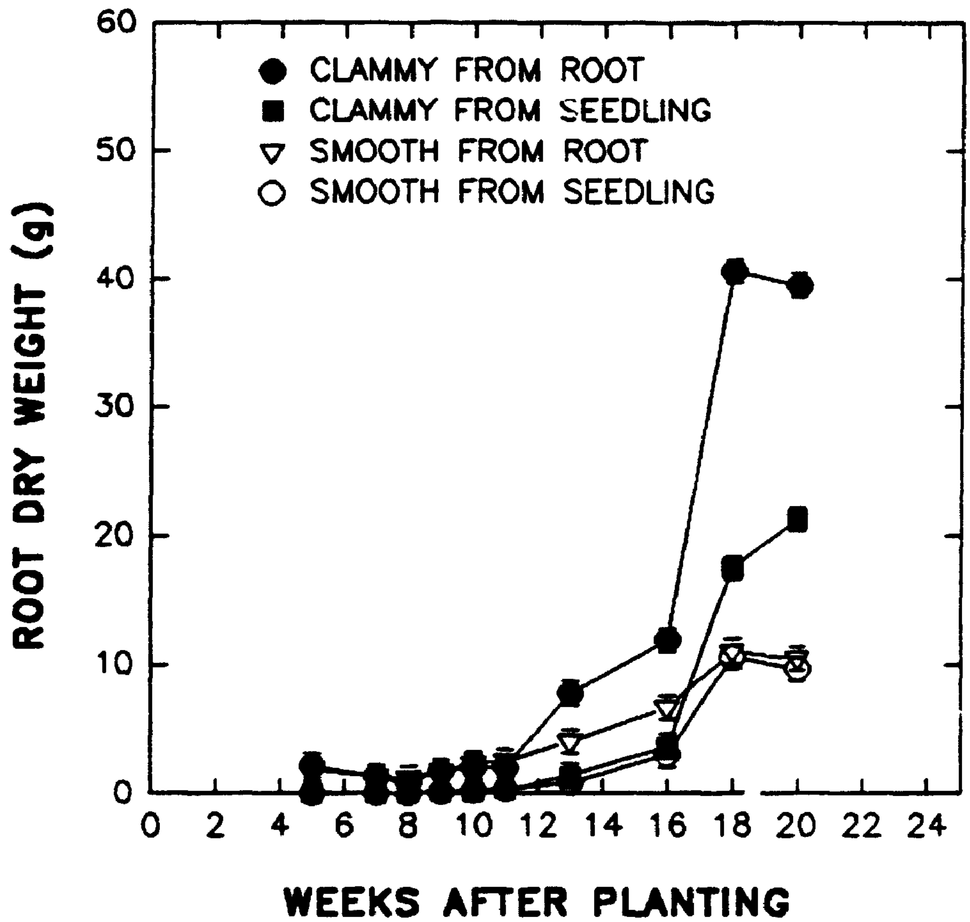
1800
1600
1400
1200
1000
800
600
400
200
0
0 2 4 6 8 10 12 14 16 18 20 22 24
CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
ROOT LENGTH cm
WEEKS AFTER PLANTING

were greater than differences between origins within species. However, plants regenerating from root fragments in both species had significantly ($p<0.05$) longer thick roots than their respective plants established from seeds. Clammy ground-cherry plants had signficantly longer thick roots ($p<0.001$) than those of smooth ground-cherry at 11 weeks after planting and thereafter. Thick root lengths grew to maxima of 1224, 690, 440, and 262 cm at 20 weeks after planting in clammy ground-cherry from root fragments, clammy ground-cherry from seedlings, smooth ground-cherry from root fragments, and smooth ground-cherry from seedlings, respectively.

Root dry weight accumulation is shown in Fig. 7. Clammy ground-cherry plants produced signficantly ($p<0.001$) greater root dry weight by 11 weeks after planting than those of smooth ground-cherry regardless of origin. These differences were maintained during the remaining harvest dates. Root-originating clammy ground-cherry plants produced significantly greater root dry weight than seed-originating clammy ground-cherry plants by 11 weeks after planting and thereafter. By the last harvest date root dry weight accumulation increased to 41.6, 21.5, 11.3, and 11.7 g in root- and seed-derived clammy ground-cherry, root- and seed-derived smooth ground-cherry plants, respectively.

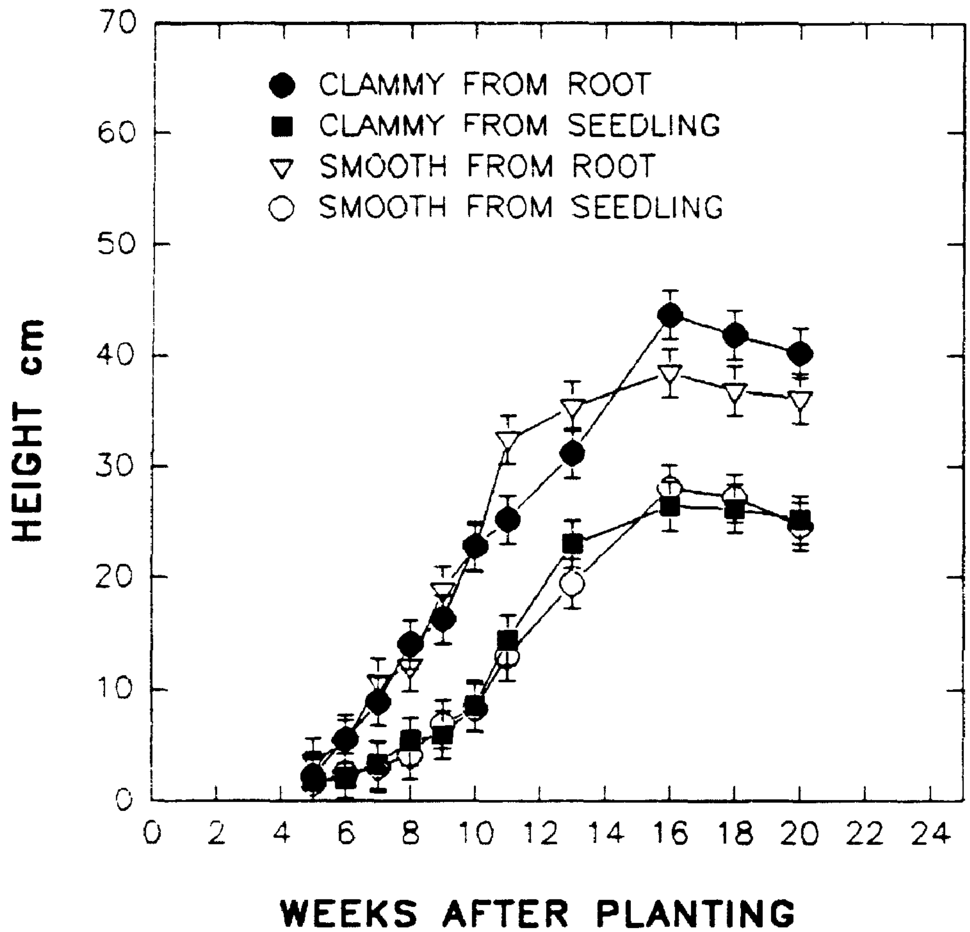
The number of below ground shoots developed by clammy and smooth ground-cherry plants during the season is shown in Fig. 8. Clammy ground-cherry plants established from root

Fig. 7. Root dry weight accumulation (± S.E) of clammy and smooth ground-cherry plants established from root fragments and from seedlings in field plots during the 1992 growing season.



CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
ROOT DRY WEIGHT (g)
WEEKS AFTER PLANTING
0
10
20
30
40
50
60
0
2
4
6
8
10
12
14
16
18
20
22
24

Fig. 8. Mean number of belowground shoots (± S.E) of clammy and smooth ground-cherry established from root fragments and from seedlings in field plots during the 1992 growing season.


CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
HEIGHT cm
0
10
20
30
40
50
60
70
0 2 4 6 8 10 12 14 16 18 20 22 24
WEEKS AFTER PLANTING

fragments gave rise to significantly ($p < 0.01$) more underground shoots than either smooth ground-cherry plants or seed-derived clammy ground-cherry plants. By October, root-derived and seed-derived clammy ground-cherry, root-derived and seed-derived smooth ground-cherry plants, had an average of 140, 58, 23 and 14 underground shoots, respectively.

In the root systems of clammy and smooth ground-cherry plants growing in cultivated fields there were fewer horizontal laterals and more deep penetrating vertical roots compared to the root systems of plants growing in experimental plots at Environmental Sciences Western.

By 16 weeks after planting about 50% of clammy ground-cherry plants originating from root fragments had four to nine satellite plants each. These satellite plants arose from horizontal laterals and were spaced about 30 to 60 cm from the main vertical root. Some of these satellite plants had flowered by early September, although these flowers did not form fruits.

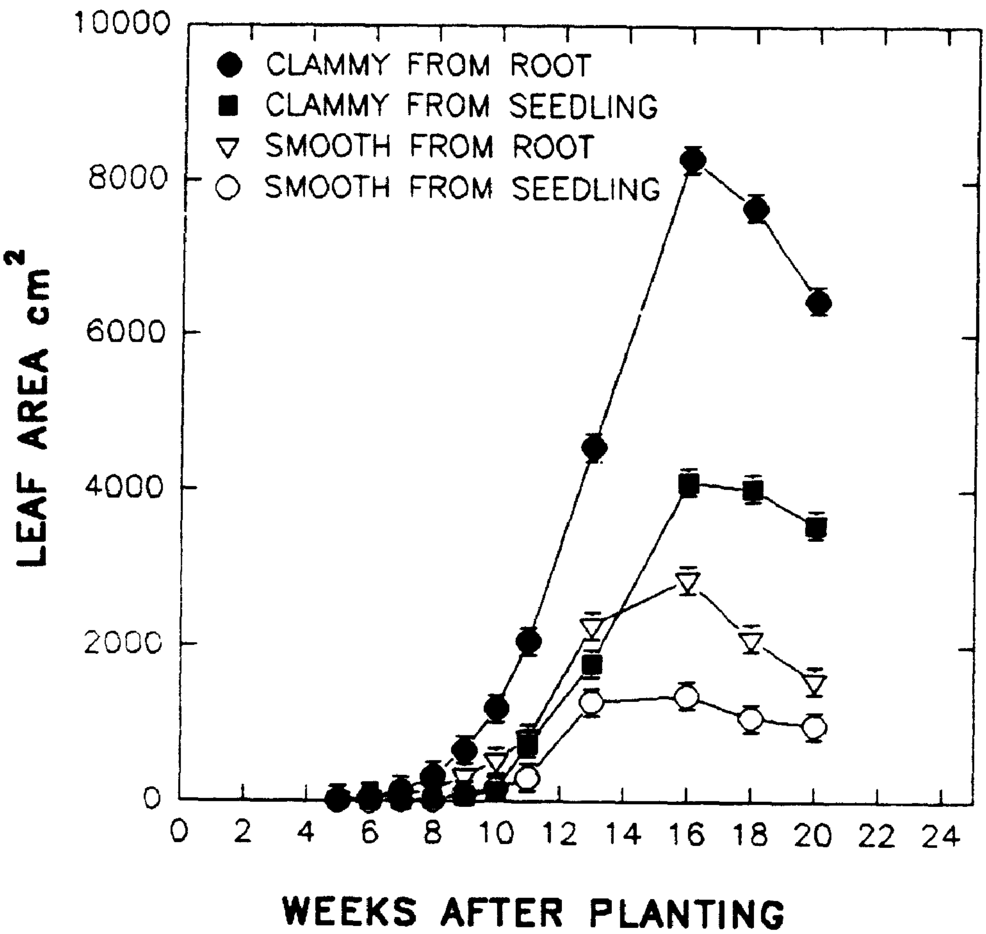
3.3.3 Shoot growth

Flower buds first appeared in clammy and smooth ground-cherry plants originating from root fragments at six and seven weeks after planting, respectively. Flowers are formed at the junction of three leaves or shoot branches. Flowers first opened in clammy and smooth ground-cherry plants from root fragments eight and nine weeks after planting, respectively. Seed-derived plants of clammy and smooth ground-cherry had their first flower buds nine and ten weeks after planting, respectively, and their first flowers opened two weeks later. Each flower lasted from five to ten days. Flowers opened at sunrise and closed at sunset. Bumble and honey bees visited the flowers each day during the growing season and served as pollinators. After fertilization the calyx enlarged to cover the developing berry. Fruits were formed in both species four weeks after the appearance of the first flower buds.

Plants of clammy ground-cherry produced significantly ($p < 0.001$) greater leaf area than those of smooth ground-cherry regardless of origin (Fig. 9). Plants grown from root fragments had significantly ($p < 0.001$) greater leaf area than those from seedlings at nine weeks following planting. Leaf area increased from 20 and 11 cm^2 at five weeks after planting to 8086 and 4113 cm^2 at 16 weeks after planting in plants of clammy ground-cherry originating from root fragments and seedlings, respectively and declined thereafter. In smooth ground-cherry, leaf area increased from 10 cm^2 at five weeks following planting, to 2205 cm^2 at 13 weeks after planting, and 1376 cm^2 at 16 weeks after planting, for root- and seed-derived plants, respectively. Plants originating from root fragments were significantly ($p < 0.01$) taller than those originating from seedlings at all harvest dates (Fig. 10).

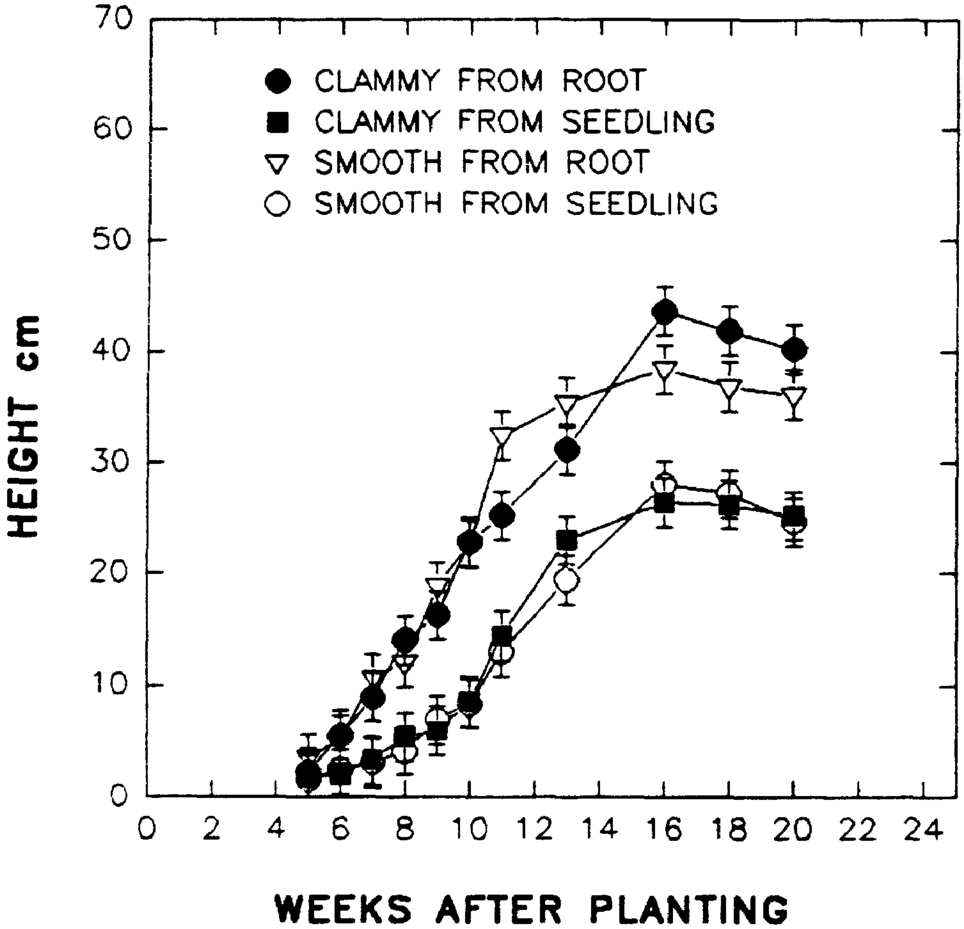
Increases in shoot dry weight corresponded to those in

Fig. 9. Mean Leaf area (± S.E) for clammy and smooth ground-cherry plants grown from root fragments and from seedlings in field plots during the 1992 growing season.



10000
8000
6000
4000
2000
0
LEAF AREA cm²
CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
0 2 4 6 8 10 12 14 16 18 20 22 24
WEEKS AFTER PLANTING

Fig. 10. Mean plant heights (± S.E) of clammy and smooth ground-cherry plants established from root fragments and from seedlings in field plots during the 1992 growing season.


CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
HEIGHT cm
70
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20 22 24
WEEKS AFTER PLANTING

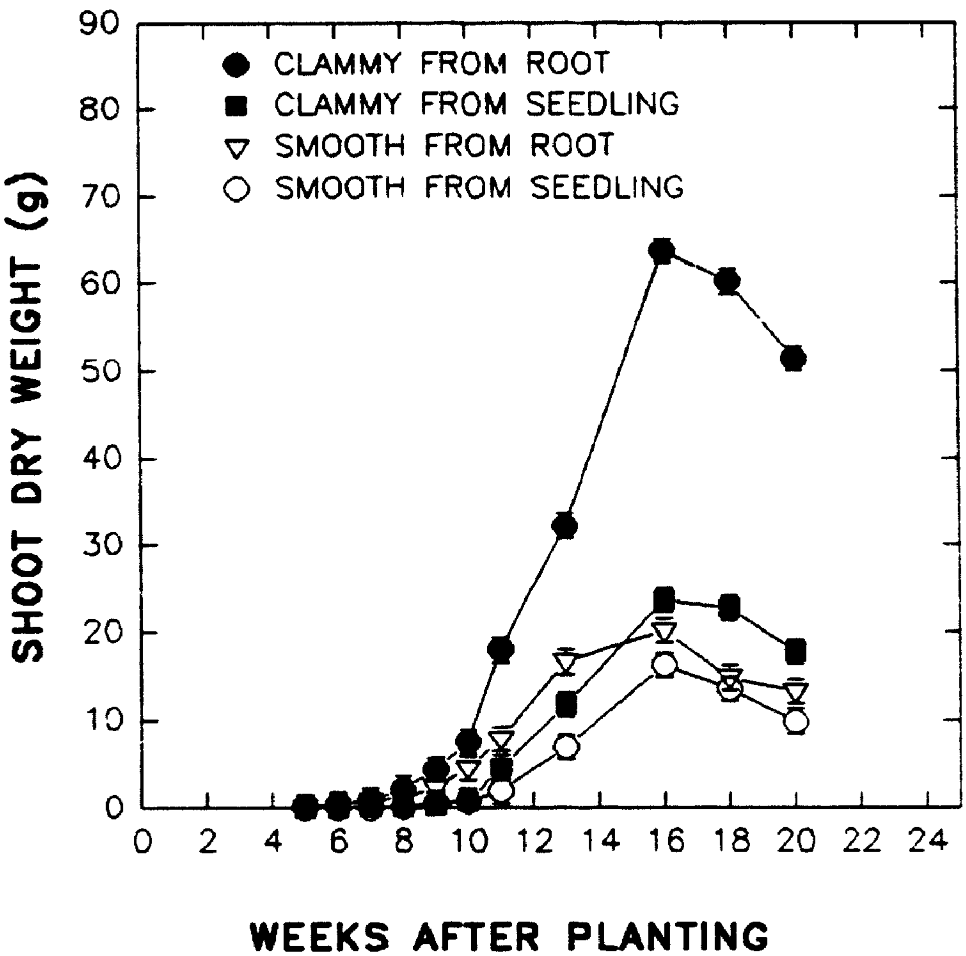
leaf area (Fig. 11). Shoot dry weight was significantly ($p < 0.001$) larger in plants of root-derived clammy ground-cherry at 11 weeks after planting, compared to seed-derived clammy ground-cherry and smooth ground-cherry regardless of origin. Shoot dry weight increased from less than 0.2 g at 5 weeks after planting to 63, 23, 20, and 16 g at 16 weeks after planting in root-derived clammy ground-cherry, seed-derived clammy ground-cherry, root-derived smooth ground-cherry, and seed-derived smooth ground-cherry, respectively, and declined thereafter (Fig. 11).

3.4 Discussion

3.4.1 Root growth

Observations on the patterns of shoot and root emergence from the root fragments showed that most shoots emerged from the proximal end, and most roots from the distal end. However, in some fragments this pattern was not observed and emergence was from any location on the root. Bloch (1943) pointed out that polarity of shoots and roots is strikingly demonstrated in regeneration of root cuttings. A stem cutting forms shoots at the apical end and roots at the basal end, whereas a root fragment regenerates roots at the apical regions and shoots at its base. Polarity of shoot and root emergence from root cuttings has been reported in a number of studies (Emery, 1955; Raju et al. 1964; Hamdoun, 1972). Schier (1973) reported that organ formation in root

Fig. 11. Shoot dry weights (± S.E) in clammy and smooth ground-cherry plants grown from root fragments and from seedlings in field plots during the 1992 growing season.


SHOOT DRY WEIGHT (g)
0
10
20
30
40
50
60
70
80
90
CLAMMY FROM ROOT
CLAMMY FROM SEEDLING
SMOOTH FROM ROOT
SMOOTH FROM SEEDLING
0 2 4 6 8 10 12 14 16 18 20 22 24
WEEKS AFTER PLANTING

fragments of *Populus tremuloides* Michx. was polar, with shoot bud formation at the proximal end and root formation at the distal end. Warmke and Warmke (1950) also observed similar polarity in root segments of *Taraxacum officinale* and *Cichorium intybus* L. In *Convolvulus arvensis* root formation was limited to the distal ends of the root fragments, whereas shoot formation, although more common on the proximal ends, occurred anywhere along the fragments (Bonnet and Torrey, 1965).

Lateral roots were formed in acropetal sequence behind the main root apex. These laterals extended either horizontally to become horizontal laterals, or followed a vertical positively geotropic growth, and also increased in thickness (long roots). Short feeding roots were initiated on the long roots. The division of roots of clammy and smooth ground-cherry into short fine roots and long thick roots follows that described and adopted for many herbaceous dicotyledons capable of regenerating vegetatively from root buds (Raju et al. 1963, 1964; Cuthbertson, 1972; Charlton, 1966). Observations that I obtained in 1990 and 1991 in Kent County, Ontario, showed that lateral root formation was more abundant on sparsely distributed, widely spaced plants of clammy ground-cherry growing in field edges, than on those growing in dense grass stands along roadsides. Roadside vegetation, is mowed periodically, suggesting that clammy ground-cherry can survive repeated mowing. In general, plants of clammy and smooth ground-cherry that were grown under competition-free conditions for experimental purposes in field plots at Environmental Sciences Western produced more lateral long roots than those growing in cultivated fields. This could be explained on the basis of reduced competition for light, soil moisture and nutrients.

In both species lateral long roots assumed vertical growth after extending 15 to 50 cm from the main shoot (Fig. 5). This change in direction of root growth has been observed in many species that regenerate from the root system (Frazier, 1943 and 1944; Raju et al ,1963 and 1964; Charlton, 1966; Rosenthal et al. 1968; Cuthbertson, 1972;). Currently, no convincing explanation is available as to why these horizontal roots change direction. One might speculate that environmental conditions and/or a shoot regulated mechanism are the underlying factors. Bonnett (1972) suggested that because of changes in soil density the root apex will often be exposed to light, and may then bend downward, and again assume horizontal growth when light is no longer received. Tepfer and Bonnett (1972) suggested a photoreceptor, presumably phytochrome, located in root tips to be involved in geotropic curvature of roots. An increase in root diameter at the bending point was associated with an increase in root bud emergence. Often a new shoot emerged at the bending site (satellite plant).

Root buds developed on both horizontal and vertical long roots (i.e roots with thicknesses about 1.5 mm or greater). More root buds were formed on horizontal long roots close to the soil surface compared to those growing at deeper depths. This might be attributed to environmental conditions in soil regions closer to the surface, such as light intensity, temperature fluctuations, oxygen concentrations, and nutrient content. In this way environmental conditions at shallow soil depths may be more conducive to bud initiation. According to Peterson (1975), light has little effect on the initiation of buds from root segments. In Hieracium florentinum application of Hoaglands's solution containing 210 ppm nitrogen to plants grown in soil resulted in more emergent root buds compared to plants treated with Hoagland's solution containing only 10.5 ppm (Peterson, 1975). Nadeau and Vanden Born (1990) working with Cirsium arvense found that in one-year-old stands the number of emerged and unemerged root buds per meter of root was higher near the soil surface in fertilized plots than in unfertilized plots. They also noted twice as many underground shoots in fertilized plots.

Clammy ground-cherry plants originating from root fragments produced satellite plants within the growing season of 1992. These satellite shoots, with their roots still connected to the parent, were capable of flowering within the same growing season. Although smooth ground-cherry plants did not produce satellite plants in 1992, my observations during 1990 and 1991 confirmed that they are capable of doing so. Satellite plants are generally disconnected from the parent shoot through decay during spring and summer, and become independent. Plants established from seedlings, however, failed to form satellite plants in their first year of growth. In greenhouse grown material, it was noted that both species could raise new shoots from the bottoms of plastic pots filled with soil to a 20 cm depth (Fig. 12).

Observations from cultivated fields near Highgate (Kent County, Ontario) indicated that smooth and clammy ground-cherry plants growing in cultivated fields had more lateral roots and root buds than those growing along roadsides or in abandoned fields. This might have resulted from the better nutrient availability and soil structure in crop fields. Clammy ground-cherry produces more horizontally growing lateral roots, whereas the root system of smooth ground-cherry penetrates deeper in* soil horizons, at least in cultivated field conditions.

Elongation of underground shoots was highest in both species in October. This agrees with results obtained by McAllister and Hederlie (1985) working with Cirsium arvense. Underground shoots formed in September and October were not only longer, but they were also larger than those developing in mid season. McIntyre (1979) suggested that competition by aerial shoots with roots for limited nitrogen resources inhibits root bud elongation. Thus, following shoot senescence in the fall underground shoots elongated to much larger sizes.

Fig. 12. Clammy (A) and smooth (B) ground-cherry shoot emergence from roots located at the bottoms of 20 cm deep plastic pots.

A

3.4.2 Shoot growth

During the first few weeks following emergence shoot growth was rather slow, but it gained momentum once a sufficient leaf area had developed (Fig. 11). The larger shoot biomass production in root-derived clammy ground-cherry plants was paralleled by a similarly large leaf area expansion. Plant height was not a good indicator of plant size (Fig. 10). This results from the rather spreading growth habit of clammy ground-cherry plants. After the 16th week following planting shoot dry weight decreased, probably because of leaf senescence. Both species were capable of flowering and setting some fruit during the growing season.

These investigations have shown that smooth and clammy ground-cherries can regenerate from root buds on intact root systems, and produce some seeds within the growing season. Baker (1965) pointed out that an ideal weed is capable of reproducing by seed and propagating vegetatively. Although neither species has become a widespread weed, they are both recognized as "problem weeds" in Southwestern Ontario (Abdullahi, 1992). In 1990 and 1991, weed populations of clammy and smooth ground-cherries emerged from overwintered roots in the first and second week of May. This was well before corn and soybean emergence, which gave the ground-cherries a competitive advantage.

CHAPTER FOUR

FACTORS AFFECTING REGENERATION FROM ROOT FRAGMENTS

4.1 INTRODUCTION

Clammy and smooth ground-cherries are perennial herbs that grow as weeds in cultivated fields and pastures (Abdullahi et al. 1991). Their resistance to control can be partially attributed to their deep and extensive root systems and to their ability to regenerate from buds produced adventitiously on their roots (Chapter 3). Root buds on the intact plants are rather inactive. However, the growth of buds is stimulated when the plants are clipped or when the root system is fragmented through cultivation (Abdullahi, unpublished).

Although seeds can produce new infestations of clammy and smooth ground-cherries, the seeds are apparently less important than the roots, which are capable of rapid and successful vegetative regeneration (Abdullahi, unpublished). In the intact plants, most shoots develop from underground stems or from the thick horizontal roots in the upper 20 cm of the soil surface. However, vertical and deep penetrating roots will also develop shoots after mechanical disturbance, e.g. cultivation, if conditions are favourable.

Fragmentation releases the root buds from the influence of parts that have been removed (McIntyre, 1972). Cutting the roots of *Euphorbia esula* stimulated the growth of buds in the region 2.5 to 5.0 cm below the cut (Coupland et al. 1955). When a clone of _Ammophila breviligulata_ Fern. was subdivided into single-node units, the proportion of buds that sprouted increased significantly compared with the non-fragmented control (Maun, 1984). In cultivated land, apical dormancy in quackgrass (_Elytrigia repens_) is often released by fragmentation of the rhizomes (Johnston and Buchholtz, 1962). Regrowth of buds after fragmentation reestablishes a few dominant aerial shoots. This system ensures a continuation of the regenerative capacity of rhizome fragments (Johnston and Bucholtz, 1962).

The capacity of root fragments to develop new shoots can be influenced by many factors. Fragment size and depth of fragment burial have been reported to affect success of regeneration (Cuthbertson, 1972; Hamdoun, 1972; Sosters and Murray, 1982; Bourdot, 1984). Differences in the regenerative capacity of root fragments, depending on their original position in the root system, have been reported in _Cirsium arvense_ (Hamdoun, 1972); _Chondrilla juncea_ (Cuthbertson, 1972); _Euphorbia esula_ (Raju et al. 1964); and _Taraxacum officinale_ (Mann and Cavers, 1979). Root fragments in a number of species were found to exhibit different regenerative capacities at different times of the year and therefore during different growth stages (e.g. _Rubus ideaus_ L. (Hudson, 1953); _Chondrilla juncea_ (Rosenthal, 1968); _Armoracia rusticana_ Gaertn. (Dore, 1953); _Euphorbia esula_ (Raju et al. 1964); _Taraxacum officinale_ (Mann and Cavers, 1979)).

Investigations on regeneration from root fragments are very limited, and in no previous research was there a comparison of regeneration from root fragments in two closely related native species living in cultivated cropland. Investigations were conducted in 1991 and 1992 to determine the effects of fragment length, depth of fragment burial, fragment orientation, plant growth stage at fragmentation, and original position of fragment on the root system, on the subsequent capacity of the root fragments to regenerate.

4.2 Materials and methods

4.2.1 Sources of material: Roots of smooth ground-cherry were excavated in 1990 from Mr. Jim Shaw's farm at Ridgetown, Ontario (42° 26′ N, 81° 54′ W). This field had been subjected to annual herbicide sprays, such as metalochlor plus atrazine, to control broad-leaved annual and perennial weeds. The roots were fragmented into 10-cm-long pieces with thicknesses ranging from 3 to 8 mm and were then planted in field plots in Environmental Sciences Western, London, Ontario (42° 59′ N, 81° 14′ W). In 1991 roots were excavated from these plots and were transplanted into a new location at Environmental Sciences Western.

In 1991 roots were dug up from a clammy ground-cherry population growing in a soybean field near Iona Station, Ontario (42° 43′ N, 81° 54′ W). This field also had been subjected to yearly herbicide application, such as imazethapyr plus linuron, to control annual and perennial weeds. The roots were cut into pieces and grown singly in plastic pots under greenhouse conditions. At the 4th-5th leaf stage the plants were transplanted into sandy loam field plots (clammy ground-cherry prefers sandy soils) at the Ridgetown College of Agricultural Technology, Ridgetown, Ontario. All fragments of clammy and smooth ground-cherry used to study the effects of fragment orientation, growth stage at fragmentation and fragment origin were obtained from these transplanted populations. For the experiments on depth of fragment burial and fragment size, smooth ground-cherry roots were obtained from Jim Shaw's farm at Ridgetown and clammy ground-cherry roots were taken from the soybean farm near Iona Station, Ontario, and were planted directly into field plots at Environmental Sciences Western. Root fragments were taken only from the first 40 cm of the vertical roots and below ground stems were excluded. Root fragment lengths were standardized at 10 cm with thicknesses ranging from 3 to 8 mm, unless otherwise stated.

4.2.2 General protocol

In the greenhouse, fragments were planted horizontally 5 cm below the soil surface in 20-cm-diameter plastic pots filled with potting soil (black muck, coarse sand, and peat moss, in proportions of 1:1:3) to 16 cm depth. The pots were watered twice daily and given a weekly fertilizer solution of NPK (20:20:20) that also delivered chelated trace elements : iron, 0.1%; manganese, 0.05%; zinc, 0.05%; boron, 0.05%; and copper, 0.02% (obtained from McRitchie Distributing, Strathroy, Ontario). In the field plots at Environmental Sciences Western (soil type: silt loam), fragments were planted 7 cm deep, in rows 50 cm apart and 50 cm space within rows. The plots were handweeded frequently.

4.2.3 Fragment orientation

Five orientations were tested:

a) horizontal

b) vertical with the proximal (proximal to the shoot) end towards the soil surface

c) vertical with the proximal end inverted

d) inclined at 45 degrees with the proximal end towards the soil surface

e) inclined at 45 degrees with the proximal end inverted.

Care was taken to make sure that at orientations other than horizontal the tip of the fragment was buried to the proper depth (i.e. 5 cm in the greenhouse and 7 cm in the field).

4.2.4 Growth stage at fragmentation

Roots were excavated, fragmented and replanted at six different growth stages:

a) at the early vegetative stage when the plants had two or three leaves (May 10)

b) at the vegetative stage when the plants had 8 to 12 leaves (June 10)

c) at flowering (June 30)

d) at fruit formation (July 24)

e) at fruit maturation (September 6)

f) at fruit dispersal (October 4).

4.2.5 <u>Different parts of the root system</u>

Root fragments were obtained from nine different parts of the root system of plants at the flowering stage (at this stage the plants have well-developed root systems with many visible buds):

a) below ground stem

b) thick horizontal root without visible buds (50 cm from main stem)

c) thick horizontal root with visible buds (50 cm from main stem)

d) horizontal root close to main stem without visible buds (0-10 cm from main stem)

e) two year old root fragments with visible buds

f) vertical root with visible buds (50 cm directly below the main stem)

g) vertical root with no visible buds (50 cm directly below the main stem)

h) thin root with no visible buds (diameter = 1.5 mm)

i) and thin root with visible buds (diameter = 1.5 mm).

4.2.6 <u>Depth of burial and size of fragment</u>

In the experiment on depth of fragment burial four depths were tested: 0 cm (i.e the fragments were left exposed on the soil surface), 5, 10 and 15 cm deep. In the experiment on fragment size four fragment lengths were studied: 2.5, 5.0, 7.5 and 10.0 cm. These fragments ranged in thickness from 3 to 8 mm.

All field experiments were conducted in the summer of 1992, except the depth of fragment burial and fragment size studies which were conducted in the summer of 1991 in field plots at Environmental Sciences Western. The experiments on orientation and time of year at fragmentation were conducted in both greenhouse and field plots. The effect of root origin was studied only in the greenhouse. In all experiments a completely randomized design was used.

4.2.7 Data recorded and analysis

In the fragment orientation, fragment origin, and growth stage at fragmentation experiments, percent regeneration, number of shoots emerged per fragment (only in the greenhouse) and days to emergence, were recorded.

For the experiments on depth of fragment burial and fragment size, the number of fragments regenerating was recorded 17, 27 and 45 days after planting. On the harvest date (August 24, 1991) plant height was measured from soil level to the growing point of the tallest shoot. Shoots were separated from roots at the soil level and were dried in an oven at 60^0 C until constant weight was obtained.

Anovas were carried out using the general linear models procedure (SAS, 1990). The hypothesis that equal proportions of regeneration would occur in the different treatments was tested using chi-squared analysis (Cox, 1987). The chi-squared analysis was conducted on the number of fragments regenerated and unregenerated out of the total planted for each treatment (20 fragments) and the results are reported as percentages.

4.3 Results

4.3.1 General: In all experiments, with the exception of those on the effects of fragment size and depth of fragment burial, the fragments were examined for patterns of shoot and root initiation. In all fragments shoots emerged before roots. Some of the root fragments that failed to regenerate had decomposed five weeks after planting, while some remained firm and apparently viable. No root fragment that produced aerial shoots decomposed completely, but some had portions that rotted away.

4.3.2 Fragment size

In both species, the first shoots emerged from 10 cm long root fragments. In clammy ground-cherry significantly higher cumulative per cent regeneration was obtained from fragments 10 cm in length than from smaller fragments (Table 1). In smooth ground-cherry there were no significant differences in total percent fragment regeneration among the different root sizes (Table 1). In clammy ground-cherry almost all fragments 10 cm in length regenerated within 27 days of planting as compared to only 25% from fragments 2.5 cm in length (Table 1). There were no significant differences among the different fragment sizes in shoot dry

Table 1. Cumulative percentage regeneration of clammy and smooth ground-cherry from root fragments of different sizes (n = 20 per treatment).

	Fragment size (cm)							
	2.5	5.0	7.5	10.0	2.5	5.0	7.5	10.0
DAP#	Clammy				Smooth			
17	10a	5a	25a	65b	25ab	35ab	15a	40b
27	25a	30a	30a	95b	50a	50a	70a	65a
45	25a	30a	40a	100b	50a	70a	70a	65a

DAP# = Days after planting.

Numbers within the same row for each species followed by the same letter are not signficantly different at the 5 % level of probability according to the chi-squared analysis.

weight per plant or plant height (Fig. 13 & Appendix 2). There was no obvious trend in shoot dry weight accumulation for fragments of different sizes of either species (Fig. 13). Although not significant, plant height increased consistently as fragment size increased in both species (Fig. 13).

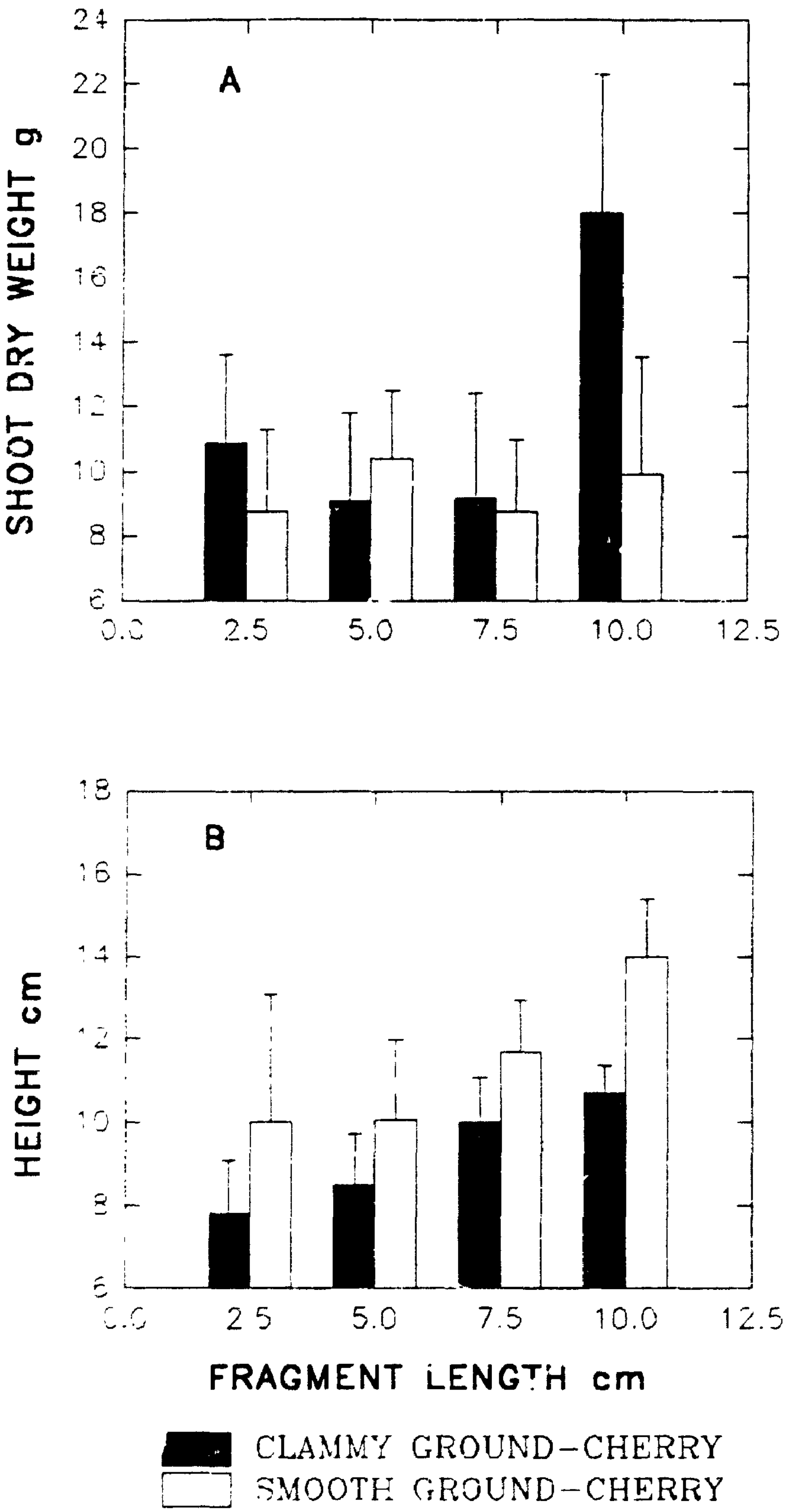
4.3.3 Depth of burial

No root fragment left at the soil surface regenerated in either species. In both species a significantly greater number of fragments buried 5 cm deep had regenerated 17 days after planting than of those buried 15 cm de(. However, this difference had disappeared 45 days after planting (Table 2). Clammy ground-cherry produced significantly more shoot dry weight than smooth ground-cherry, regardless of depth of fragment burial (Fig. 14 A & Appendix 2). There were no significant differences in plant height among the different treatments (Fig. 14 B).

4.3.4 Fragment orientation

Orientation had no significant effect on the capacity of root fragments to regenerate in either species (Table 3). Clammy ground-cherry root fragments took significantly longer to regenerate in the greenhouse than those of smooth ground-cherry regardless of planting orientation (Tables 4 & 5, Appendix 3), but this difference was not seen in field results (Table 5). Fragment orientation had no significant effect on time taken to regenerate nor on the number of

Fig. 13 The effects of root fragment length on: (A) shoot dry weight (± S.D), and (B) height (± S.D) of clammy and smooth ground-cherry grown in field plots, 11 weeks after planting.



A
SHOOT DRY WEIGHT g
24
22
20
18
16
14
12
10
8
6
0.0
2.5
5.0
7.5
10.0
12.5
B
HEIGHT cm
18
16
14
12
10
8
6
0.0
2.5
5.0
7.5
10.0
12.5
FRAGMENT LENGTH cm
CLAMMY GROUND-CHERRY
SMOOTH GROUND-CHERRY

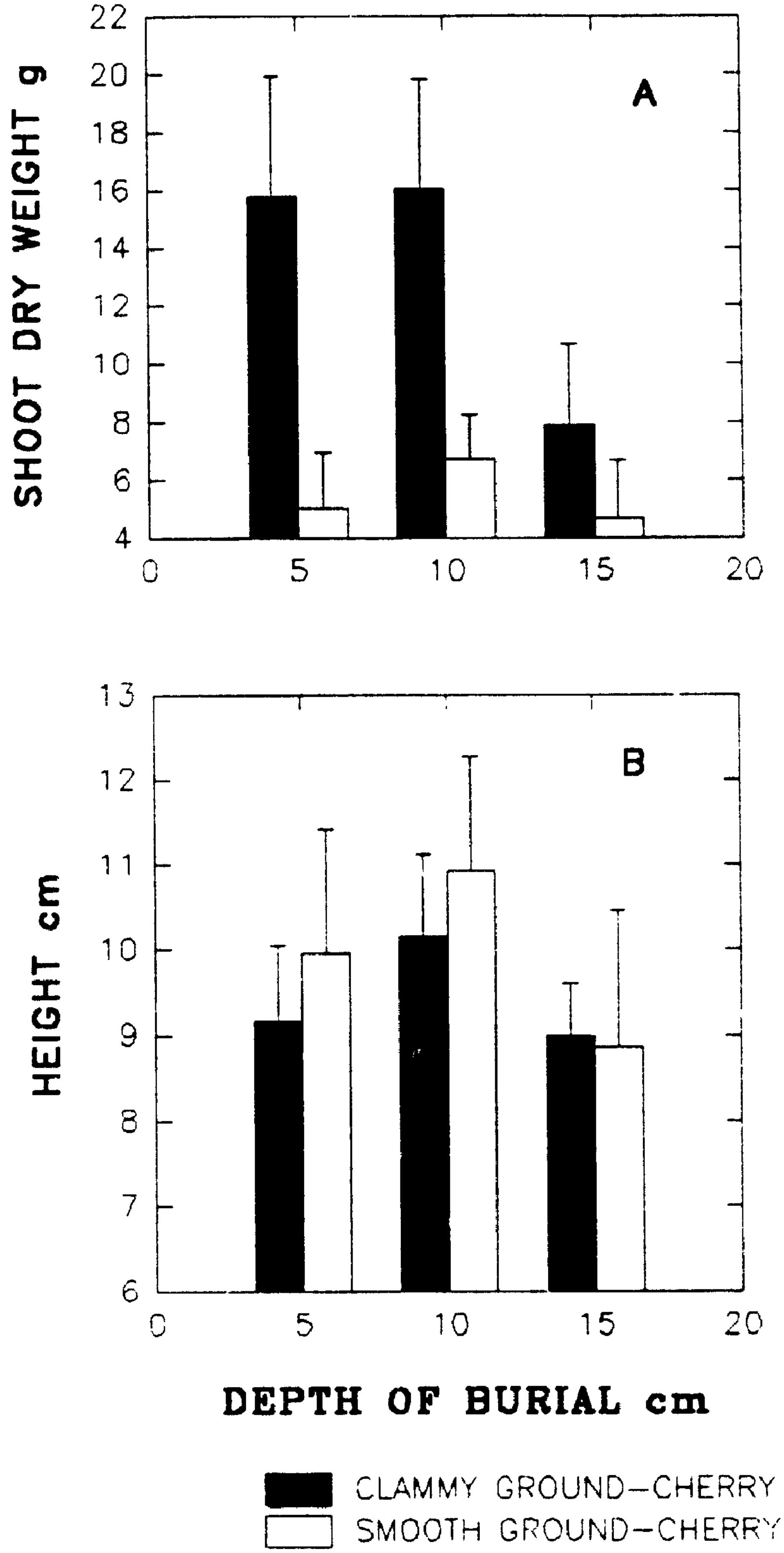
Table 2. Cumulative percentage emergence of clammy and smooth ground-cherry root fragments planted at different depths (n = 20 per treatment).

	Clammy			Smooth		
Depth (cm):	5	10	15	5	10	15
DAP#						
17	55a	15b	5b	30a	15ab	5bc
27	60a	40a	5b	75a	40a	15b
45	60a	60a	45a	75a	70a	65a

DAP = Days after planting.

Numbers within the same row for each species followed by the same letter are not significantly different at the 5% level of probability according to chi-squared analysis.

Fig. 14 The effects of depth of burial of root fragments on: (A) shoot dry weight (± S.D), and (B) height (± S.D) of clammy and smooth ground-cherry grown in field plots, 11 weeks after planting.



SHOOT DRY WEIGHT g
A
22
20
18
16
14
12
10
8
6
4
0
5
10
15
20
HEIGHT cm
B
13
12
11
10
9
8
7
6
0
5
10
15
20
DEPTH OF BURIAL cm
CLAMMY GROUND-CHERRY
SMOOTH GROUND-CHERRY

Table 3. Effect of orientation of root fragments on their subsequent capacity to regenerate (n= 20 per treatment)

	Percent regenerating			
	Greenhouse		Field	
	CGC*	SGC	CGC	SGC
Fragment orientation				
1. Horizontal	100	100	70	75
2. Vertical with proximal end uninverted	95	95	85	75
3. Vertical with proximal end inverted	90	90	60	60
4. At 45 degrees to the horizontal, proximal end uninverted	85	100	55	85
5. At 45 degrees to the horizontal, proximal end inverted	75	95	75	70

* CGC = Clammy ground-cherry

SGC = Smooth ground-cherry

There were no significant differences among the different orientations in percent regeneration according to the chi-squared analysis.

Table 4. Effects of root fragment orientation on mean number of days (± S.E) to emergence, and mean number of shoots per plant (± S.E) 3 weeks after planting, of clammy and smooth ground-cherry (greenhouse experiment).

	Days to emergence	Shoots
Species (means)		
Clammy	14.09 (0.36)	1.56 (0.06)
Smooth	8.21 (0.34)	1.09 (0.07)
Orientation (means)		
Horizontal	10.53 (0.53)	1.40 (0.10)
Vertical uninverted	11.58 (0.54)	1.37 (0.10)
Vertical inverted	12.22 (0.55)	1.25 (0.10)
45 degrees not inverted	11.02 (0.55)	1.39 (0.11)
45 degrees inverted	10.19 (0.58)	1.23 (0.11)
Species x orientation (means)		
CGC[#] - horizontal	13.10 (0.76)	1.70 (0.14)
CGC - vertical uninverted	15.26 (0.76)	1.73 (0.14)
CGC - vertical inverted	16.11 (0.78)	1.50 (0.14)
CGC - 45 degrees uninverted	14.23 (0.80)	1.50 (0.14)
CGC - 45 degrees inverted	11.33 (0.86)	1.38 (0.14)
SGC - horizontal	7.95 (0.74)	1.02 (0.14)
SGC - vertical uninverted	7.89 (0.76)	1.00 (0.14)

Table 4 continued:

	Days to emergence	Shoots
SGC - vertical inverted	8.33 (0.78)	1.00 (0.14)
SGC - 45 degrees uninverted	7.80 (0.741)	1.29 (0.147)
SGC - 45 degrees inverted	9.05 (0.782)	1.06 (0.157)

CGC, SGC = clammy and smooth ground-cherry respectively.

Table 5. Effects of root fragment orientation on mean number of days to emergence (± S.E) of clammy and smooth ground-cherry (field experiment) n= 20 per treatment.

	Days to emergence
Species (means)	
Clammy	22.47 (0.53)
Smooth	23.01 (0.54)
Orientation (means)	
Horizontal	25.81 (0.84)
Vertical uninverted	22.75 (0.82)
Vertical inverted	23.06 (0.86)
45 degrees uninverted	24.79 (0.84)
45 degrees inverted	24.78 (0.84)
Species x orientation (means)	
CGC[#] - horizontal	22.43 (1.22)
CGC - vertical uninverted	21.70 (1.10)
CGC - vertical inverted	21.87 (1.33)
CGC - 45 degrees uninverted	23.41 (1.31)
CGC - 45 degrees inverted	22.93 (1.17)
SGC - horizontal	26.20 (1.17)
SGC - vertical uninverted	20.78 (1.21)

Table 5 continued:

	Days to emergence
SGC - vertical inverted	21.25 (1.31)
SGC - 45 degrees uninverted	23.17 (1.099)
SGC - 45 degrees inverted	23.64 (1.211)

CGC, SGC = clammy and smooth ground-cherry respectively.

emerged shoots per root fragment (Tables 4 & 5). Root fragments with preformed visible buds at planting time regenerated faster than those with no preformed buds.

Examination of the root fragments four to five weeks after planting indicated that the site of shoot emergence from a fragment generally depended on the location of visible buds prior to planting. However, in root fragments with no preformed visible buds more shoots developed from the proximal end (closer to the crown) and more roots from the distal end.

4.3.5 Growth stage

The proportion of root fragments regenerated from plants sampled at different growth stages is shown in Table 6. In both species significantly fewer root fragments sampled from plants at the fruit dispersal stage regenerated in the same season compared to those obtained in the early vegetative stage (Table 6). In the field, no fragment obtained from plants dispersing fruit (in October) regenerated in the same year (Table 6). In the fruit maturation sampling fewer fragments of clammy ground-cherry regenerated in the field compared to those of smooth ground-cherry.

In both greenhouse and field plots smooth ground-cherry shoots emerged faster than those of clammy ground-cherry (Tables 7, 8 & Appendix 4). There were no significant differences between the two species in the number of shoots

Table 6. Percent regeneration of root fragments of clammy and smooth ground-cherry sampled at different growth stages, in greenhouse and field plots (n= 20 per treatment). This does not include regeneration in field plots after overwintering.

	Greenhouse		Field	
	CGC#	SGC	CGC	SGC
Growth stage				
Early vegetative	100a*	100a	70a	55bc
Vegetative	100a	85ab	85a	65ab
Flowering	85ab	95a	75a	75ab
Fruiting	70b	90ab	90a	90a
Fruit maturation	90a	85ab	30b	70ab
Fruit dispersal	60b	65b	0	0

* Numbers within the same column followed by the same letter are not significantly different at 5% level of probability.

CGC, SGC = clammy and smooth ground-cherry respectively.

Table 7. Effects of growth stage at root fragmentation on mean number of days to emergence (± S.E), and mean number of shoots (± S.E) 3 weeks after planting, per plant of clammy and smooth ground-cherry (greenhouse experiment) n= 20 per treatment.

	Days to emergence	Mean number of shoots
Species (mean)		
Clammy	11.82 (0.29)	1.77 (0.08)
Smooth	9.82 (0.28)	1.64 (0.08)
Growth stage (means)		
Early vegetative	7.20 (0.45)	2.07 (0.13)
Vegetative	9.18 (0.47)	1.75 (0.14)
Flowering	8.71 (0.48)	1.75 (0.14)
Fruiting	12.54 (0.51)	1.70 (0.15)
Fruit maturation	13.29 (0.48)	1.63 (0.14)
Fruit dispersal	14.03 (0.59)	1.32 (0.17)
Species x growth stage (means)		
Clammy - early vegetative	8.10 (0.64)	2.15 (0.18)
Clammy - vegetative	9.20 (0.64)	2.20 (0.18)
Clammy - flowering	9.47 (0.70)	1.80 (0.20)
Clammy - fruiting	14.64 (0.77)	1.57 (0.22)
Clammy - fruit maturation	14.17 (0.68)	1.61 (0.19)
Clammy - fruit dispersal	15.36 (0.86)	1.27 (0.25)

Table 7 continued:

	Days to emergence	Mean number of shoots
Smooth - early vegetative	6.30 (0.64)	2.00 (0.18)
Smooth - vegetative	9.18 (0.69)	1.29 (0.20)
Smooth - flowering	7.90 (0.66)	1.68 (0.19)
Smooth - fruiting	10.44 (0.68)	1.83 (0.195)
Smooth - fruit maturation	12.41 (0.70)	1.65 (0.200)
Smooth - fruit dispersal	12.69 (0.80)	1.38 (0.229)

Table 8. Effect of growth stage at root fragmentation on mean number of days to emergence (± S.E), of clammy and smooth ground-cherry (field experiment) n= 20 per treatment.

	Days to emergence
Species (mean)	
Clammy	19.79 (0.52)
Smooth	18.05 (0.48)
Growth stage (means)	
Early vegetative	21.70 (0.81)
Vegetative	20.00 (0.72)
Flowering	19.73 (0.73)
Fruiting	16.47 (0.67)
Fruit maturation	16.71 (0.98)
Fruit dispersal	-------------
Species x growth stage (means)	
Clammy - early vegetative	21.21 (1.07)
Clammy - vegetative	18.70 (0.97)
Clammy - flowering	21.20 (1.0[illegible])
Clammy - fruiting	19.83 (0.04)
Clammy - fruit maturation	18.00 (1.63)
Clammy - fruit dispersal	-------------

Table 8 continued

	Days to emergence
Smooth - early vegetative	22.18 (1.21)
Smooth - vegetative	21.29 (1.07)
Smooth - flowering	18.27 (1.033)
Smooth - fruiting	13.11 (0.943)
Smooth - fruit maturation	15.43 (1.069)
Smooth - fruit dispersal	-------------

developed per root fragment (Table 7 & Appendix 4). Significant differences were observed among the different growth stages in time from planting to shoot emergence (Tables 7, 8 and Appendix 4). In the greenhouse, roots sampled at the early vegetative stage (when the plants had two to three leaves) regenerated in about a week, whereas roots sampled at the beginning of fruit formation and thereafter took about twice as long to regenerate. The pattern observed on time taken for fragments to regenerate in the field was the reverse of that in the greenhouse. This probably resulted from the rather dry weather early in the season and the greater rainfall in the later summer months recorded for Environmental Sciences Western in 1992. In the field clammy ground-cherry roots regenerated most quickly when sampled from plants at the fruit maturation stage, and smooth ground-cherry roots regenerated most quickly when sampled at the fruit formation stage (Table 8). In the greenhouse both species regenerated most rapidly from fragments sampled at the two-to-three leaf stage (Table 7). Shoots emerging from root fragments sampled at the fruiting, the fruit maturation and fruit dispersal stages grew more slowly than those from roots sampled at preceding stages.

4.3.6 Root origin

The percent regeneration of root fragments from different parts of the root system is shown in Table 9. Ninety-one percent and 96% of root fragments with visible

Table 9. Effect of origin of root fragments on their subsequent capacity to regenerate in smooth and clammy groundcherry n= 20 per treatment. Greenhouse experiment.

Origin of rootstock	Percent emerged clammy	Percent emerged smooth
A. Belowground stem	80ab	100a
B. Thick horizontal root without buds (50 cm from main stem)	65bc	60b
C. Thick horizontal root with buds	100a	95a
D. Root close to main stem without buds (0-10 cm from main stem)	35c	35b
E. Old root fragment with buds	85ab	90a
F. Vertical root without buds (50 cm deep)	50c	60b
G. Vertical root with buds (50 cm deep)	100a	100a
H. Thin root with no buds Diameter = 1.5 mm	45c	35b
I. Thin root with buds Diameter = 1.5 mm	90a	95a

* Numbers within the same column followed by the same letter are not significantly different at the 5% level of probability according to the chi-squared analysis.

buds regenerated in clammy and smooth ground-cherries respectively; whereas only about 48% of those without visible buds did so in either species. Root fragments as thin as 1.5 mm diameter regenerated almost completely if they had preformed visible buds at planting and about 40% regenerated if they had no preformed buds at planting. Root fragments from two year old root systems also had high regenerative capacity.

Root fragments of smooth ground-cherry developed shoots faster than those of clammy ground-cherry when averaged over all treatments, but the latter species developed significantly more shoots per root fragment than the former (Table 10). Root fragments with visible buds produced shoots faster than those without visible buds. The origin of the root fragment had no significant effect on the number of shoots emerging from it (Table 10 & Appendix 5). In the thick root category, fragments taken 50 cm deep from the vertical taproot were the last to regenerate in both species. Thin root fragments (diameter = 1.5 mm) with no visible buds took about 20 days to produce shoots.

4.4 Discussion

4.4.1 Fragment size

Fragments 10 cm long regenerated faster than smaller fragments in clammy ground-cherry, whereas there was no obvious pattern in the rapidity of emergence in smooth ground-cherry. Smooth ground-cherry may be less dependent

Table 10. Effects of origin of root fragments on mean number of days to emergence (± S.E), and mean number of shoots per plant (± S.E) of clammy and smooth ground-cherry (greenhouse experiment) n= 20 per treatment. #

	Days to emergence	Shoots per plant
Species (mean)		
Clammy	10.02 (0.27)	1.27 (0.05)
Smooth	9.04 (0.27)	1.12 (0.05)
Root origin (means)		
A. Belowground stem w/b	8.31 (0.48)	1.37 (0.08)
C. Thick horiz. root w/b	7.22 (0.46)	1.23 (0.08)
D. Root Close to main n/b	8.71 (0.77)	1.00 (0.14)
E. Old root fragment w/b	7.88 (0.46)	1.32 (0.08)
F. Vertical root n/b	10.90 (0.61)	1.19 (0.11)
G. Vertical root w/b	7.03 (0.45)	1.37 (0.08)
H. Thin root n/b	20.68 (0.72)	1.00 (0.17)
I. Thin root w/b	7.16 (0.46)	1.00 (0.08)
Species - origin (means)		
Clammy - A	9.56 (0.72)	1.43 (0.13)
Clammy - B	6.38 (0.79)	1.46 (0.14)
Clammy - C	7.45 (0.64)	1.30 (0.11)

Table 10 continued:

	Days to emergence	Shoots per plant
Clammy - D	10.14 (1.08)	1.00 (0.19)
Clammy - E	8.82 (0.69)	1.41 (0.12)
Clammy - F	12.30 (0.91)	1.30 (0.16)
Clammy - G	7.45 (0.64)	1.50 (0.11)
Clammy - H	21.22 (0.95)	1.00 (0.17)
Clammy - I	6.84 (0.66)	1.00 (0.12)
Smooth - A	7.05 (0.64)	1.30 (0.11)
Smooth - B	9.33 (0.74)	1.06 (0.13)
Smooth - C	7.00 (0.66)	1.16 (0.12)
Smooth - D	7.29 (1.08)	1.00 (0.19)
Smooth - E	6.94 (0.68)	1.22 (0.12)
Smooth - F	9.50 (0.83)	1.08 (0.15)
Smooth - G	6.60 (0.64)	1.25 (0.11)
Smooth - H	20.14 (1.08)	1.00 (0.19)
Smooth - I	7.47 (0.66)	1.00 (0.12)

horiz. = horizontal

n/b = no visible buds

w/b = with visible buds

For more detailed explanation of categories see Table 9.

on size of fragment for regeneration than clammy ground-cherry. The significance of a larger fragment, (e.g. 10 cm) is that it contains larger food reserves and generally more root buds compared to a smaller fragment. However, it is evident from the results that more plants of clammy or smooth ground-cherry will be obtained by cutting a given length of the root system into many small units compared to a few large units. Similar results have been reported for other species. Hamdoun (1972) working on *Cirsium arvense* found that the longer the root fragment the greater the number producing shoots. Root fragments of *Saponaria officinalis* L. 5 cm or longer were more likely to produce buds than those of 2.5 cm length (Lubke and Cavers, 1970).

4.4.2 Depth of burial

The results indicated that both species were capable of regenerating from the depths considered, except at the soil surface, where no fragment survived because of desiccation. Although fragments buried 5 cm deep developed shoots faster than those buried 15 cm deep during the first three weeks; 45% and 65% of fragments buried at 15 cm depth had regenerated 45 days after planting in clammy and smooth ground-cherries respectively. Similar findings were reported for other species capable of sprouting from below ground organs. Hamdoun (1972) noted a considerable reduction in shoot production of *Cirsium arvense* at planting depths greater than 10 cm. Swanton (1986) found that time taken for shoots to emerge from rhizome fragments and tubers of *Helianthus tuberosus* L. increased with planting depth. In the rhizomatous species *Achillea millefolium* L. no shoots emerged from fragments left on the soil surface (Bourdot, 1984). No sprouting was observed on *Sorghum halepense* L. rhizome fragments or on tubers of *Cyperus rotundus* L. after a week of air drying (Horowitz, 1972).

The results of the effects of fragment size and depth of fragment burial indicated that under field conditions both species are capable of reproducing from root fragments as short as 2.5 cm and can raise new shoots from fragments buried at a depth of 15 cm. This implies that cultivation will spread these species into uninfested fields through contaminated agricultural machinery. However, the failure of root fragments left on the soil surface to survive indicates that tillage can eliminate some fragments by exposing them to drying conditions.

4.4.3 Fragment orientation

Both the greenhouse and field results supported the hypothesis that planting orientation has no significant effect on the capacity of root fragments to regenerate, other than differences due to random fluctuations. This indicates that both species will be capable of regenerating from root fragments after tillage operations no matter how the fragments are repositioned in the soil, provided they are covered. In a few cases shoots developing from preformed visible buds took longer to emerge from the soil, when the buds were located on a section of the root that was oriented upside down, e.g. in vertical and at 45° orientations. My results agree with those of Richardson (1975) working on Rubus procerus Muell. who reported that shoots occurred at any position along the root segments, although a greater number of shoots emerged from the proximal end.

4.4.4 Growth stage

Both species have the potential to regenerate from root pieces during any growth stage if conditions are favourable. The low sprouting capacity recorded for clammy ground-cherry in the field at the fruit maturation stage (September) may suggest that this species is more sensitive to the declining temperatures and shortening photoperiod. In Southwestern Ontario, most shoots of clammy ground-cherry die before those of smooth ground-cherry, which remain alive until late November. A number of researchers working on other species capable of regenerating from root sections (Dore, 1953; Raju et al. 1964; Cuthbertson, 1972; Mann and Cavers, 1979) observed decreased shoot emergence from roots sampled during the flowering stage. On the other hand, Monson and Davis (1964), working on Euphorbia esula, found a high incidence of emergence at all sampling dates, which is in agreement with my results. It is difficult to draw recommendations from these results on control by tillage since neither species lost the ability to regenerate. Some root fragments planted in the late summer of 1989 for multiplication were capable of overwintering and developing shoots in the next spring. Tillage might, however, reduce the chances of sprouting if it is conducted during drier periods of the growing season, or during cold weather, by leaving the fragments on the soil surface, provided soil erosion is kept reasonably low.

4.4.5 Root origin

Although twice as many root fragments with visible buds regenerated as those without visible buds, the results show that both species have the potential to establish from root fragments irrespective of the presence of preformed visible buds. Root fragments obtained from 50 cm deep on the vertical root had fewer buds than those originating closer to the soil surface. The lack of significant differences among root fragments of different origins in the number of emerged shoots per root fragment implies establishment of correlative bud inhibition (Johnston and Buchholtz, 1962). Raju et al. (1964) noted that root fragments of *Euphorbia esula* from different depths had extensive regenerative capacity, regardless of the presence of preformed buds. In *Cirsium arvense* 88% of the root fragments with visible buds produced shoots compared to 72% from fragments with no visible buds (Hamdoun, 1972). Hamdoun also reported 73% regeneration in mature root fragments compared to 7.5% from young roots. The significance of the low regenerative ability of the horizontal roots close to the main stem in both species is probably to maintain a certain minimum distance between shoots arising from the same parent, so that competition for resources such as light, water and mineral nutrients is kept low. In both species new aerial daughter shoots do not emerge until the parent plant has passed the flower bud formation stage, and then at a spacing of about 30 cm from the parent plant.

CHAPTER FIVE

EFFECT OF HERBICIDES ON SMOOTH GROUND-CHERRY

5.1 INTRODUCTION

Smooth ground-cherry is a perennial herb native to Canada and the United States (Gleason, 1963). It regenerates from deep fleshy root systems and reproduces by seeds. In recent years in Southwestern Ontario there has been an increase in the number of crop fields infested by persistent populations of ground-cherries, particularly smooth ground-cherry. Smooth ground-cherry grows in corn, soybean and tomato fields, and in pastures. In some crop fields in southwestern Ontario, farmers have failed to control smooth ground-cherry with herbicides. During trips to Kent, Elgin and Middlesex Counties, Ontario, I have observed some crop fields with smooth ground-cherry as the dominant weed. Shifts in weed populations often occur as a result of human production practices, when certain species are controlled to the exclusion of others. Repeated applications with a limited number of herbicides can result in the predominance of a more resistant flora (Chancellor, 1979).

Skrotch et al. (1975) noted that the percentage of brambles (*Rubus* sp.) and *Clematis virginiana* L. in the weed populations of apple orchards increased after five yearly applications of 2.2 and 4.5 kg ha^{-1} of terbacil (3-tert-butyl-5-chloro-6-methyluracil). In winter cereals, the need to control Alopecurus myosuroides Huds. led to the sole use of substituted ureas (Makepeace, 1982). The result has been that hitherto unfamiliar weeds have become serious pests e.g Veronica persica L. and Galium aparine L. (Makepeace, 1982). Weber et al. (1974) evaluated changes in weed populations resulting from three consecutive annual applications of fluorometuron [1,1-dimethyl-3-(alpha,alpha,alpha-trifluro-m-tolyle)urea], prometryn [2,4-bis(isopropylamino)-6-(methylthio)-s-triazine], and trifluralin [alpha,alpha,alpha-trifluro-2,6-dinitro-N,N-dipropyl-p-toluidine], at typical rates. In all cases the proportion of Cyperus esculentus L., a perennial, increased while susceptible annual species decreased. Koch (1964) noted that repeated applications of DNOC (2-methyl-4-6-dinitrophenol) over a period of three years resulted in a reduction of Sinapis arvensis Small, Polygonum convolvulus L. and Galium aparine and a sizable increase in resistant Alopecurus myosuroides.

The increased infestations of smooth ground-cherry can also be attributed to the increased use of reduced tillage in North America. Reduced tillage can lead to an increase in perennial species. Zero tillage in corn in the midwest and southeast portions of the United States led to an increase in honeyvine milkweed (Aldrich, 1984). Reduction or elimination of tillage favours the higher competitive ability of perennial weeds. The accumulation of crop residues may also block herbicides from reaching the target plants (Aldrich, 1984).

There is a lack of information on the effects of herbicides on plants regenerating from root fragments. In some investigations where root fragments were used, emphasis was on translocation of herbicides to the underground system without looking at the overall effects of herbicides on the root system (Gottrup et al. 1976; Sardberg et al. 1980; McAllister and Haderlie, 1985; Zollinger et al. 1992;). In others, established populations were sprayed , i.e plants were not regenerated from root fragments (Schultz and Burnside, 1979; Cramer and Burnside, 1981; Gulling and Arnold, 1985; Donald, 1992). Some researchers grew their plants from root fragments but measured only the effects of the herbicides on the shoots (Parochetti, 1974; Frank et al. 1993).

Glyphosate is a non-selective, postemergence, herbicide that has effectively controlled many perennial weeds (Gottrup et al. 1976; Rioux et al. 1974). It is translocated through the leaves. Atrazine is widely used as a selective herbicide for control of broad-leaved weeds and grasses (Anonymous, 1979). Kil-Mor is a mixture of herbicides with hormone-type effects on plants, used to control broad-leaved weeds (Anonymous, 1992). Bentazon is a postemergence, foliarly translocated herbicide used for the control of broad-leaved weeds. These herbicides were selected for this study because they are recommended in Ontario for the control of broad-leaved weeds (Anonymous, 1992).

The objectives of this investigation were to:

a) study the effects of four commonly used herbicides, each applied at three rates, on plants of smooth ground-cherry established from root fragments.

b) derive control measures for this persistent weed.

I selected smooth ground-cherry for this investigation because in field crops near London smooth ground-cherry is a more aggressive weed than clammy ground-cherry, which is confined to border rows. Furthermore, there is a lack of published reports on the response of smooth ground-cherry to herbicides. The persistence of smooth ground-cherry in cultivated fields subjected to annual herbicide applications might be explained, at least in part, by tolerance to herbicides.

5.2 Materials and methods

5.2.1 Greenhouse.

In June 1989, root systems of smooth ground-cherry were obtained from a population growing in Mr. Rudy Brown's corn field near Highgate, Ontario (42° 30′ N, 81° 49′ W). Weeds growing in the field had been sprayed annually with herbicides. The roots of smooth ground-cherry were cut into 10 cm long fragments and planted immediately in plots at the University of Western Ontario Field Station (Environmental

Sciences Western) near London, Ontario. The plots were kept weed-free. On May 6, 1991 roots were dug up from these plots, taken to the greenhouse and cleaned with tap water. The roots were then fragmented to 10 cm long pieces with thicknesses ranging from 3 to 8 mm. The number of buds and fresh weight were recorded for each fragment. One hundred and twenty fragments were planted singly at 5 cm depth in 20 cm wide plastic pots filled with greenhouse potting soil (black muck loam, coarse sand, peatmoss in proportions of 1:1:3). Each pot was labelled as to the number of buds and fresh weight of the root fragment. The pots were arranged randomly on rectangular benches in the greenhouse. The pots were watered twice daily, and given a weekly fertilizer solution of NPK (20:20:20) that also contained chelated trace elements: iron, 0.1%; manganese, 0.05%; zinc, 0.05%; boron, 0.05%; and copper, 0.02%. The greenhouse was maintained at 20° and 27° C during night and day respectively with a 14 hour photoperiod.

Ten days after shoot emergence, 78 pots that had the most vigorous and homogenous plants were selected and the remainder were discarded. On the appearance of the first flower buds, three weeks after emergence, the pots were taken to the Agriculture Canada Research Station, London, Ontario, and four herbicides: atrazine (2-chloro-4-(ethylamino)-6-isopropylamino)-s-triazine); bentazon (3-isopropyl-1H-2,1,3-benzothiadiazine-(4)3H-one 2,2-dioxide); glyphosate (N-(phosphonomethyl)glycine); and Kil-Mor [a mixture of 2,4-D (2,4-dichlorophenoxy)acetic acid; mecoprop 2{(4-chloro-o-totyl)oxy}propionic acid, and dicamba (3,6-dichloro-o-anisic acid) in the proportions 61:16:23, respectively] were sprayed, each at 3 rates, on six pots (total sprayed 72). Six unsprayed pots were also transported with the treated pots and served as controls. The herbicides rates used were atrazine at 0.28, 0.56, and 1.12 kg active ingredient (ai) ha^{-1}; glyphosate at 0.31, 0.63, and 1.25 kg ai ha^{-1}; bentazon at 0.137, 0.275 and 0.550 kg ai ha^{-1} plus 21 ha^{-1} of assist concentrate (mineral oil surfactant) for each rate; and Kil-Mor at 0.066, 0.133 and 0.265 kg ai ha^{-1}. The highest rate for each herbicide corresponds to approximately half the rate recommended by the manufacturer.

Occasionally,these rates will be referred to as the low, medium and high rates respectively. The herbicides were delivered to the plants in a closed chamber with an overhead automatic cycle sprayer using a flat fan nozzle, Teejet #8004, at a speed of 100 KPH and a pressure of 172 Kpa. The plants were returned to the greenhouse immediately after spraying.

Data were recorded weekly on number of flowers and flower buds, number of axilary branches and plant height. The plants were harvested 5 weeks after spraying. Harvested plants were divided into stems, leaves and roots and dried in an oven at 60 degrees Celsius until constant weight was achieved. The data were analyzed as a factorial unbalanced randomized design using the general linear models Anova procedures of the Statistical Analysis Systems (SAS, 1990). To separate means, t-tests were used.

5.2.2 Field station.

On May 23, 1991 roots were excavated from the same field plots at Environmental Sciences Western as were used for the greenhouse experiment. The roots were washed with tap water and cut into fragments each 10 cm long with diameters ranging from 3 to 10 mm. The number of buds and fresh weight were recorded for each fragment. The root fragments were then planted 7 cm deep in 39 double-row plots in the field, each 6 m long with 0.40 m between rows and 1.25 m spacing between double rows. The experimental design was a randomized complete block design with 3 blocks (13 double-rows per block) leaving 1.5 m spacing between blocks. Between May 24 and May 28, 1991 twenty root fragments were planted in each row, with 0.30 m between fragments (total root fragments planted = 1560). The plots were handweeded as needed. The number of plants emerging and days to emergence were recorded. On July 12, 1991, when about 50% of the plants had developed the first flower buds and had 6 to 9 leaves, four herbicides, glyphosate, atrazine, bentazon, and Kil-mor were each applied at three rates to the plots, employing an air-pressurized bicycle sprayer that was pushed over the plant rows with 300 l/ha spray volume and 275 Kpa pressure. The herbicide application rates were: 0.62, 1.25 and 2.50 kg ai ha^{-1} of glyphosate; 0.56, 1.12 and 2.24 kg ai ha^{-1} of atrazine; 0.28, 0.56, and 1.12 kg ai ha^{-1} of bentazon; 0.13, 0.27 and 0.54 kg ai ha^{-1} of Kil-mor. Plants were checked frequently for developing symptoms and the number surviving was noted four weeks after spraying.

Six weeks after spraying, four randomly selected plants were harvested from each plot. The harvested plants were divided into roots, leaves, stems, and reproductive parts (flowers and fruits) and the weight for each plant part was determined after drying in an oven at 60° C to constant weight. The data were analysed using the general linear models of the Statistical Analysis Systems (SAS, 1990). Means were compared by using t-tests.

5.3 **Results**

5.3.1 Greenhouse

Most of the root fragments had developed shoots five to six days after planting. All root fragments developed shoots. Data on root fragment fresh weight, number of buds per root fragment (before planting) and days to emergence are shown in Appendix 6. The Pearson correlation showed that time to emergence was not correlated to either root fragment fresh weight or number of buds (Table 11).

The first symptoms of herbicide injury were observed three days after spraying, in plants treated with Kil-Mor. Plants treated with Kil-Mor had twisted shoot branches and curled leaves. Younger leaves of plants treated with glyphosate turned chlorotic seven days after spraying, but

Table 11. Pearson Correlation Coefficients for root fragment fresh weight (before planting), number of buds (before planting), and days to emergence of smooth ground-cherry (greenhouse experiment) # .

	Weight per fragment	Number of buds	Days to emergence
Weight	1.000	-0.0218	0.0195
	0.0	0.8150	0.8342
Buds	-0.0218	1.000	-0.0545
	0.8150	0.0	0.5578
Days	0.0195	-0.0545	1.000
	0.8342	0.5578	0.0

Of the paired numbers, the top number is a measure of the strength of relationship between variables and the lower one is the probability of observing a correlation coefficient as large or larger than the one obtained by chance alone (that is, when the variables in question actually have zero correlation) (Cody and Smith, 1991).

the lower leaves had no obvious symptoms. Bentazon and atrazine treated plants had chlorotic leaves seven and ten days after treatment respectively. In atrazine treated plants, this leaf chlorosis developed into necrosis on leaf margins two weeks after treatment, while in bentazon treatments only plants which received the high rate did so and at a much slower pace.

All plants that received glyphosate at 1.25 kg ha^{-1} died two to three weeks after spraying, while only one of those receiving glyphosate at 0.63 kg ha^{-1} was killed within three weeks of treatment. Two plants treated with atrazine at 1.12 kg/ha and three plants treated with atrazine at 0.56 kg ha^{-1} were dead three weeks after spraying.

The Anova results are summarized in Appendix 7. Plant height, number of axillary branches per plant and number of flowers per plant are shown for treated and control plants in Figs. 15, 16 and 17, respectively. Bentazon applied at 0.14 kg ha^{-1} and atrazine at 0.28 kg ha^{-1} had no significant effect on the rate of height increase (Fig. 15). In contrast, increases in plant height were checked significantly in plants treated with Kil-Mor and glyphosate, regardless of application rates (Fig. 15). A rate of 1.25 kg ha^{-1} glyphosate completely stopped shoot growth one week following spraying, and bentazon at 0.56 kg/ha and Kil-Mor at 0.27 kg ha^{-1} significantly reduced plant height three weeks following treatment (Fig. 15). The effect of the herbicides at each rate on the number of branches and number

Fig. 15. The effect of four herbicides each at three rates on plant height (± S.E) of smooth ground-cherry during five weeks following herbicide application. Note that with glyphosate all plants were killed by the highest rate by 3 weeks. See Methods and Materials for the actual rates (greenhouse experiment).

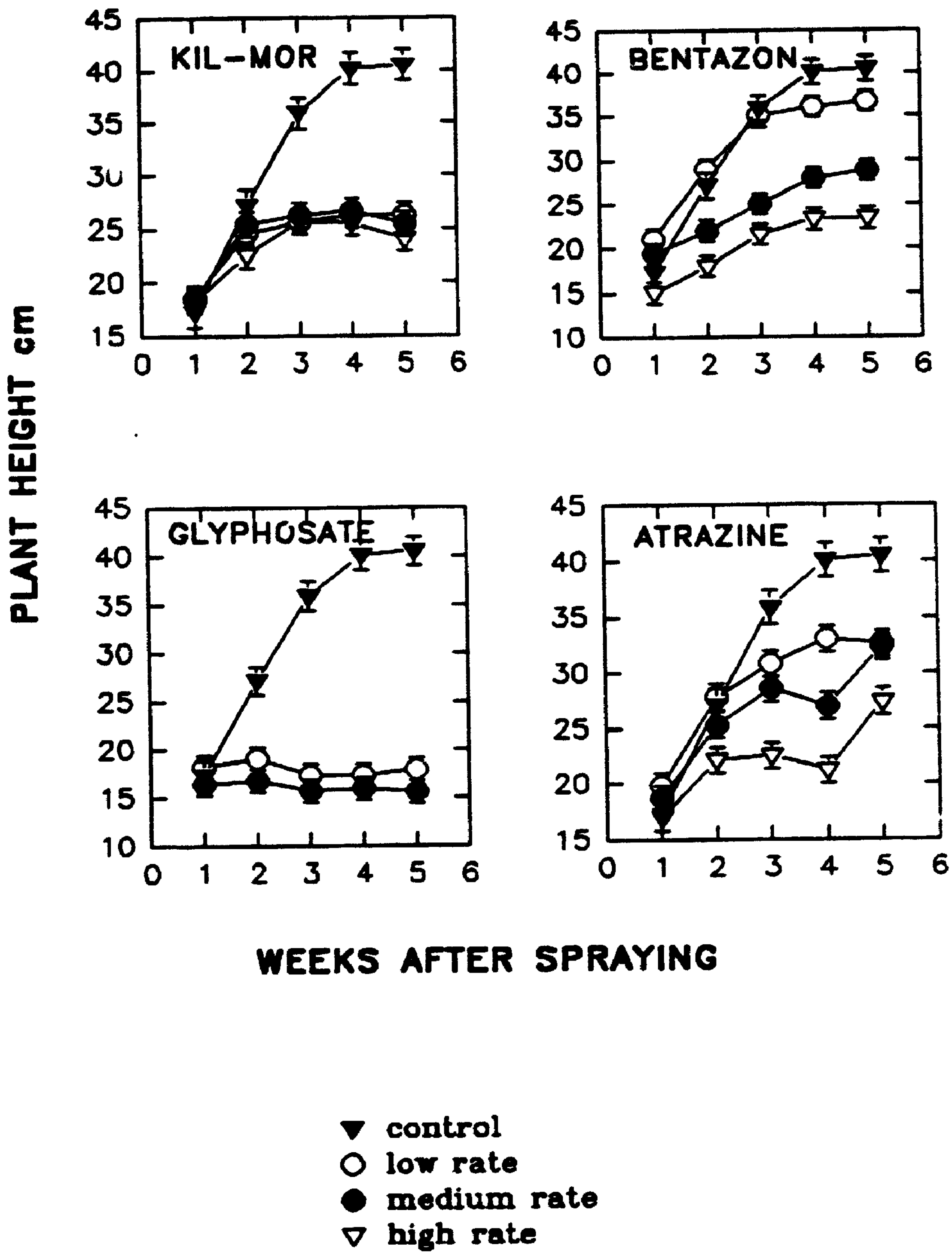

KIL-MOR
BENTAZON
GLYPHOSATE
ATRAZINE
PLANT HEIGHT cm
WEEKS AFTER SPRAYING
control
low rate
medium rate
high rate

Fig.16 The effect of four herbicides each at three rates on the number of branches (± S.E) per plant of smooth ground-cherry during 5 weeks following herbicide application. Note that with glyphosate all plants were killed by the highest rate by 3 weeks. See Methods and Materials for actual rates used (greenhouse experiment).

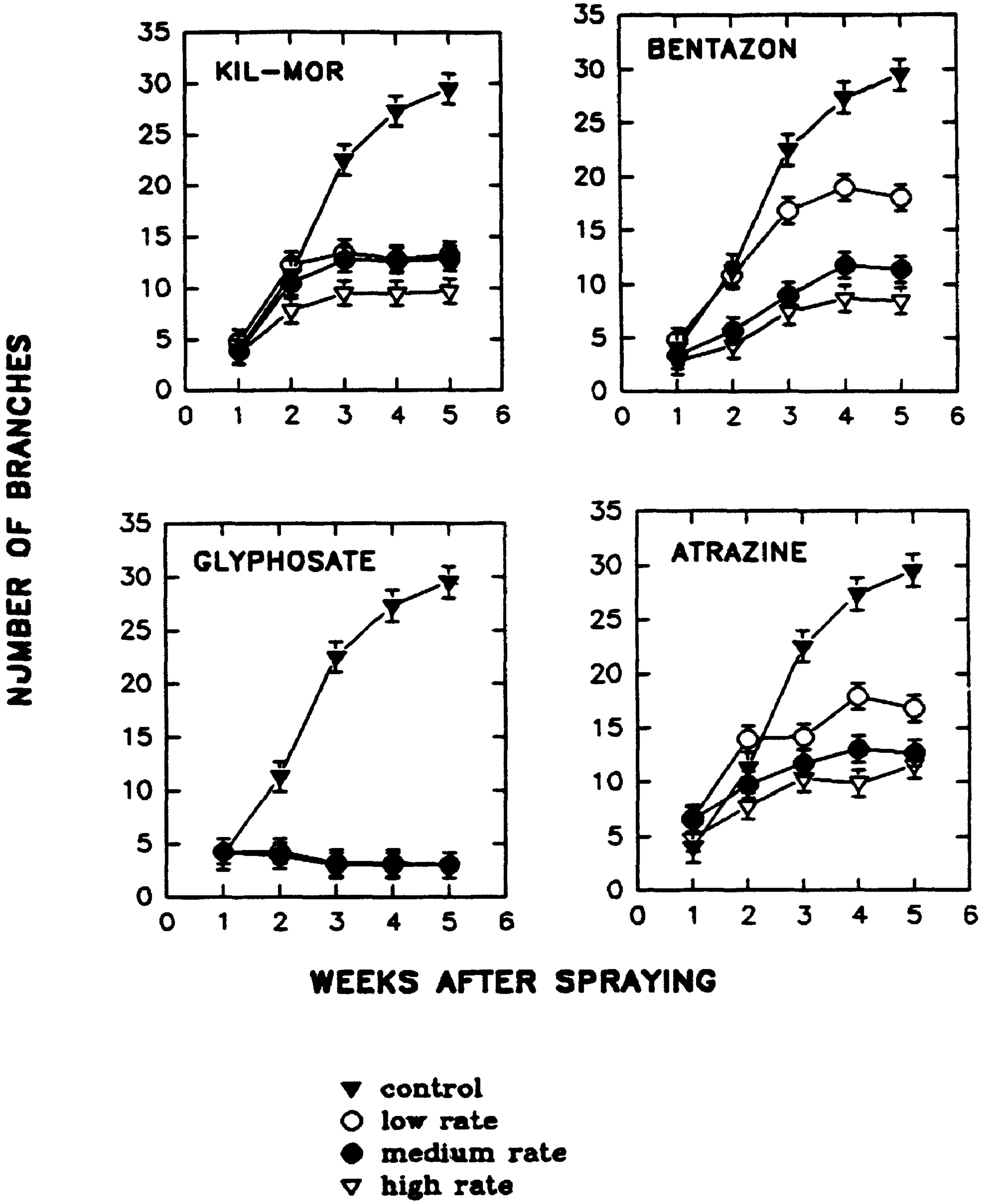
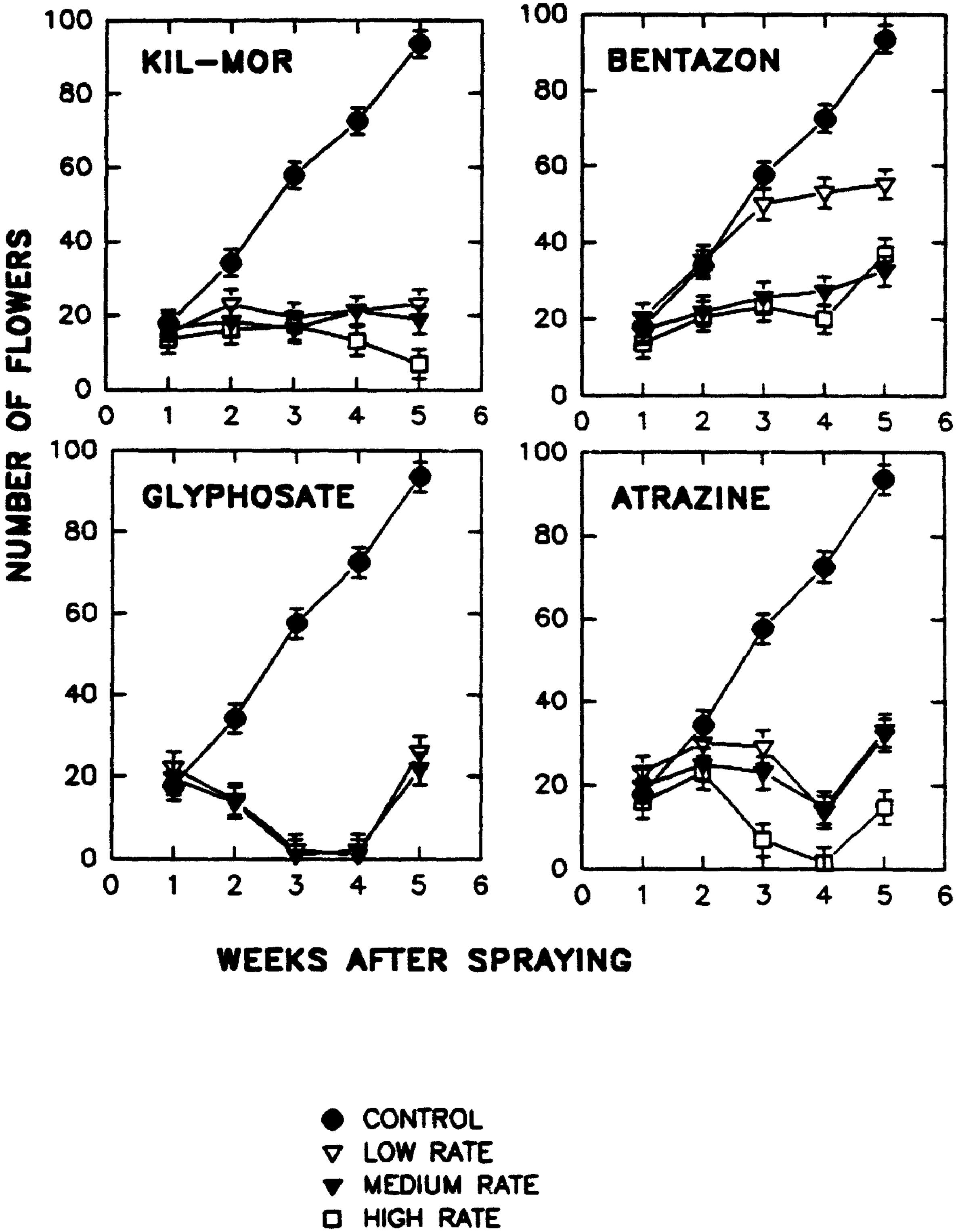

KIL-MOR
BENTAZON
GLYPHOSATE
ATRAZINE
NUMBER OF BRANCHES
WEEKS AFTER SPRAYING
0
5
10
15
20
25
30
35
0
1
2
3
4
5
6
control
low rate
medium rate
high rate

Fig. 17. The effect of four herbicides each at three rates on the number of flowers per plant (± S.E) of smooth ground-cherry during 5 weeks following herbicide application. Note that with glyphosate all plants were killed by the highest rate by 3 weeks. See Methods and Materials for the actual rates used (Greenhouse experiment).

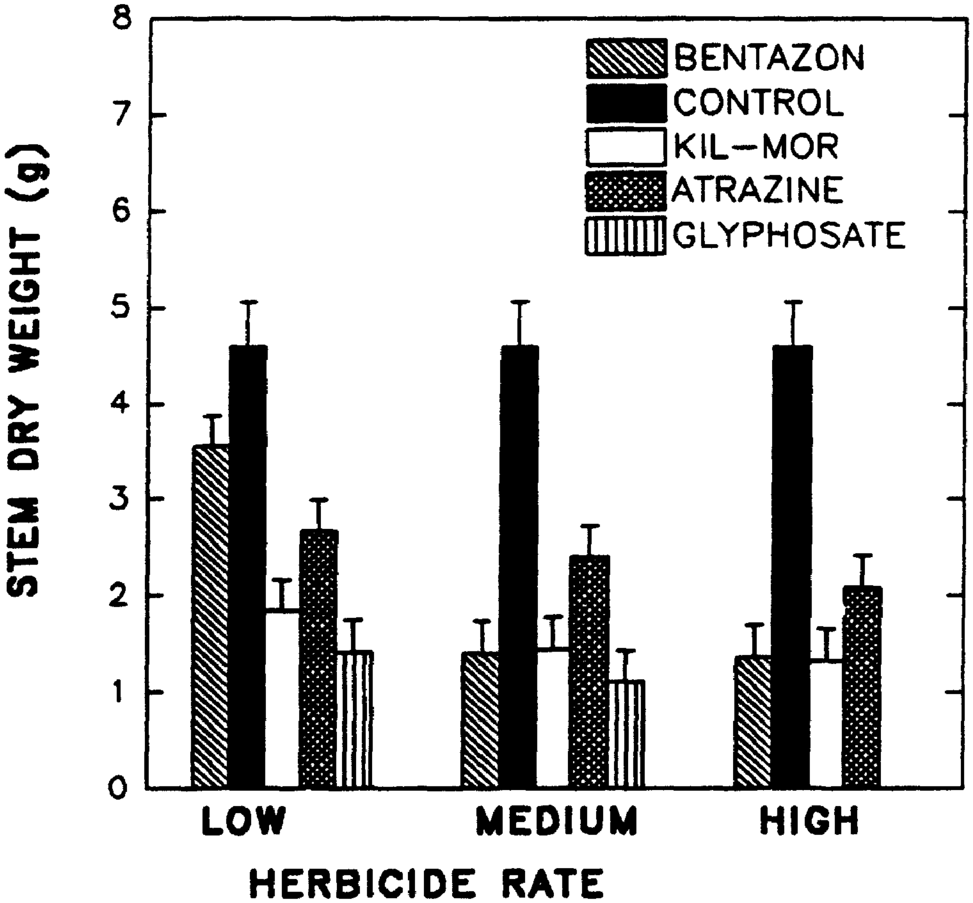

KIL-MOR
BENTAZON
GLYPHOSATE
ATRAZINE
NUMBER OF FLOWERS
WEEKS AFTER SPRAYING
0
20
40
60
80
100
0
1
2
3
4
5
6
CONTROL
LOW RATE
MEDIUM RATE
HIGH RATE

of flowers showed a pattern similar to that described for plant height (Figs. 16 and 17). At the high rates of application all herbicides significantly slowed the rate of increase of branches and flowers (Figs. 16 and 17). Atrazine applied at 0.56, and 1.12 kg ha^{-1} reduced stem dry weight by an average of 70% and glyphosate at 0.31 and 0.63 kg ha^{-1} reduced stem dry weight by an average of 76% (Fig. 18). Bentazon and Kil-mor applied at both the medium and high rates each reduced stem dry weight by about 73%. Atrazine reduced leaf dry weight by 83 to 89% across all rat^s of application Fig. 19). Glyphosate was as effective as atrazine in reducing leaf dry weight. Bentazon at 0.28 and 0.56 kg ha^{-1} resulted in an average of 62% reduction of leaf dry weight (Fig. 19), while Kil-Mor caused a 57% reduction of leaf dry weight across all rates of application. Atrazine reduced root dry weight by 70% across all rates, whereas glyphosate had signficant effects on root dry weight when applied at 0.63 and 1.25 kg ha^{-1} (Fig. 20). Kil-Mor applications resulted in 30% reduction of root dry weight regardless of rate and bentazon applied at 0.28, and 0.56 kg ha^{-1} reduced root dry weight by an average of 44% (Fig. 20).

5.3.2 Field station

Shoots had emerged from most of the root fragments by 20 to 28 days after planting (Appendix 8). The total percentage emergence was about 85% in all plots. The Pearson

Fig. 18. The effect of four herbicides each applied at three rates, on stem dry weight (± S.E) of smooth ground-cherry. The low, medium, and high rates used for each herbicide were: atrazine- 0.28, 0.56 and 1.12 kg ha^{-1}; glyphosate- 0.31, 0.63 and 1.25 kg ha^{-1}; bentazon- 0.14, 0.28 and 0.56 kg ha^{-1}; kil-mor- 0.07, 0.14 and 0.28 kg ha^{-1}. The control was plotted with the medium and high rates for comparison.



STEM DRY WEIGHT (g)
0
1
2
3
4
5
6
7
8
BENTAZON
CONTROL
KIL-MOR
ATRAZINE
GLYPHOSATE
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 19. The effect of four herbicides, each applied at three rates, on leaf dry weight (± S.E) of smooth ground-cherry. The low, medium and high rates used for each herbicide were: atrazine- 0.28, 0.56 and 1.12 kg ha^{-1}; glyphosate- 0.31, 0.63 and 1.25 kg ha^{-1}; bentazon- 0.14, 0.28 and 0.56 kg ha^{-1}; kil-mor- 0.07, 0.14 and 0.28 kg ha^{-1}. The control was plotted with the medium and high rates for comparison.

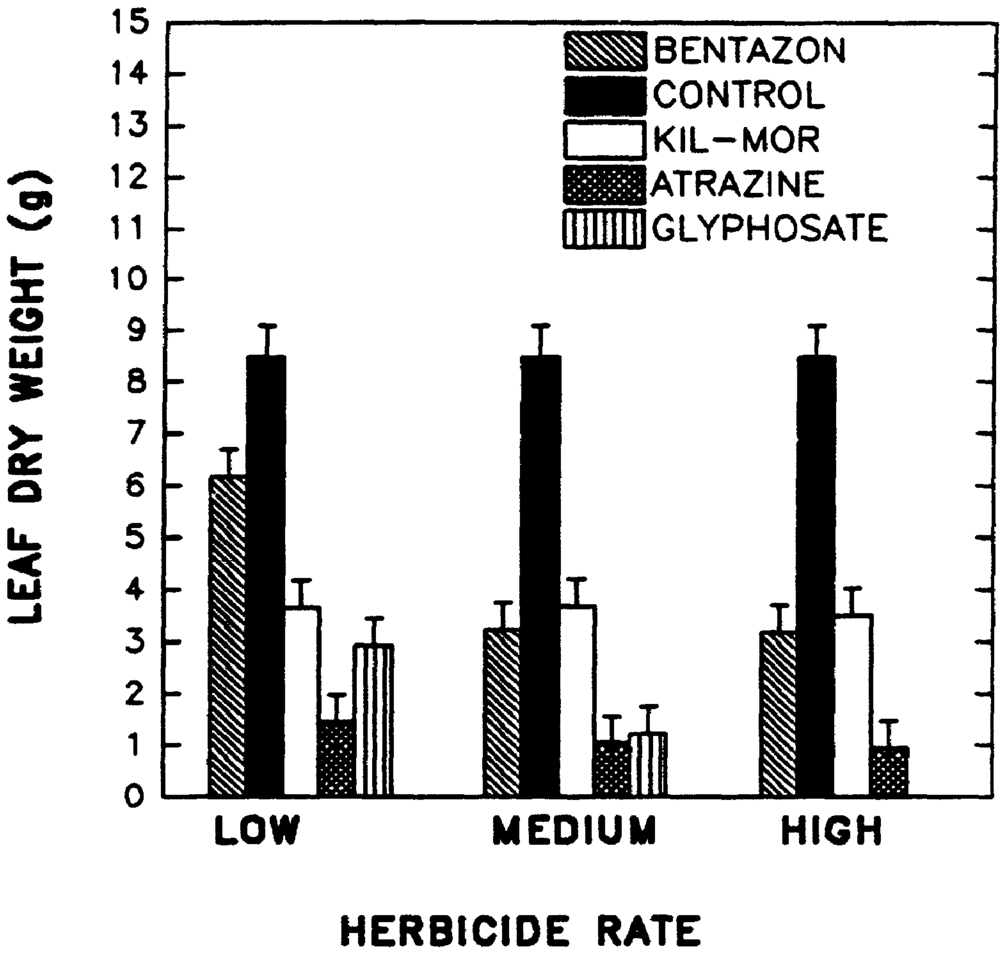
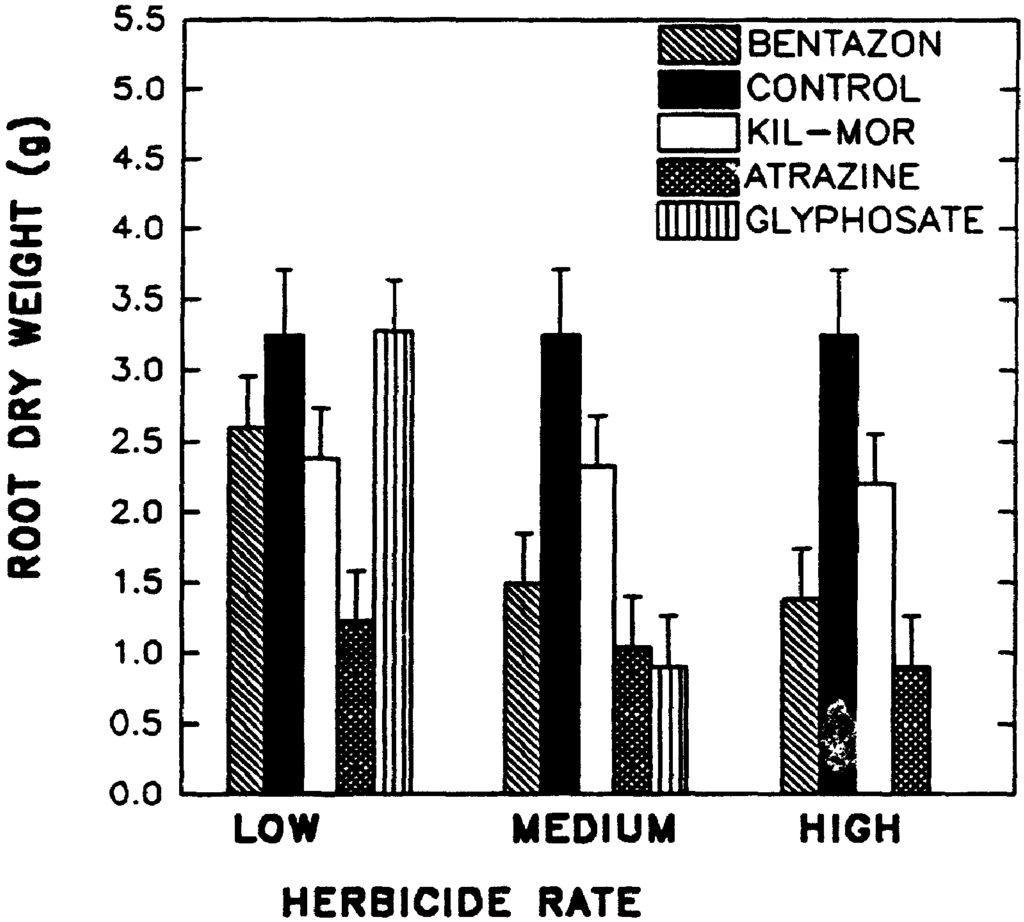

BENTAZON
CONTROL
KIL-MOR
ATRAZINE
GLYPHOSATE
LEAF DRY WEIGHT (g)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 20. The effect of four herbicides, each applied at three rates, on root dry weight (± S.E) of smooth ground-cherry. The low, medium and high rates used for each herbicide were: atrazine- 0.28, 0.56 and 1.12 kg ha^{-1}; glyphosate- 0.31, 0.63 and 1.25 kg ha^{-1}; bentazon- 0.14, 0.28 and 0.56 kg ha^{-1}; kil-mor- 0.07, 0.14 and 0.28 kg ha^{-1}. The control was plotted with the medium and high rates for comparison.



ROOT DRY WEIGHT (g)
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
BENTAZON
CONTROL
KIL-MOR
ATRAZINE
GLYPHOSATE
LOW
MEDIUM
HIGH
HERBICIDE RATE

correlation coefficient showed no correlation between days to emergence and either root fresh weight or number of buds per root fragment (Table 12).

The first symptoms of herbicide damage were noted in plants treated with Kil-Mor. They developed symptoms similar to those observed in the greenhouse, but much less pronounced. The upper young leaves of plants treated with glyphosate developed leaf chlorosis, although much less severe than that observed in the greenhouse. Older leaves of glyphosate-treated plants had no apparent symptoms of injury. Plants sprayed with atrazine at 2.24 kg ha^{-1} developed leaf chlorosis and necrosis within two to three weeks, but at lower rates of application atrazine-treated plants did not show any damage symptoms. Plants receiving bentazon at 1.12 kg ha^{-1} showed mild leaf chlorosis three weeks after spraying. The percentage of plants surviving four weeks following treatment is shown in Table 3. Only glyphosate and atrazine, applied at 2.50 and 2.24 kg ha^{-1} respectively, reduced plant density significantly (Table 13).

A summary of Anova results is shown in Appendix 7. Plant height was negatively affected by glyphosate regardless of rate of application and by atrazine at the 2.24 kg ha^{-1} rate of application only (Fig 21). Atrazine applied at 0.56 and 1.12 kg ha^{-1} had a stimulating effect on shoot elongation (Fig. 21). Both glyphosate and atrazine applied at the high rates, significantly checked axillary

Table 12. Pearson Correlation Coefficients, for root fragment fresh weight (before planting), number of buds (before planting) and days to emergence of smooth ground-cherry (field experiment)

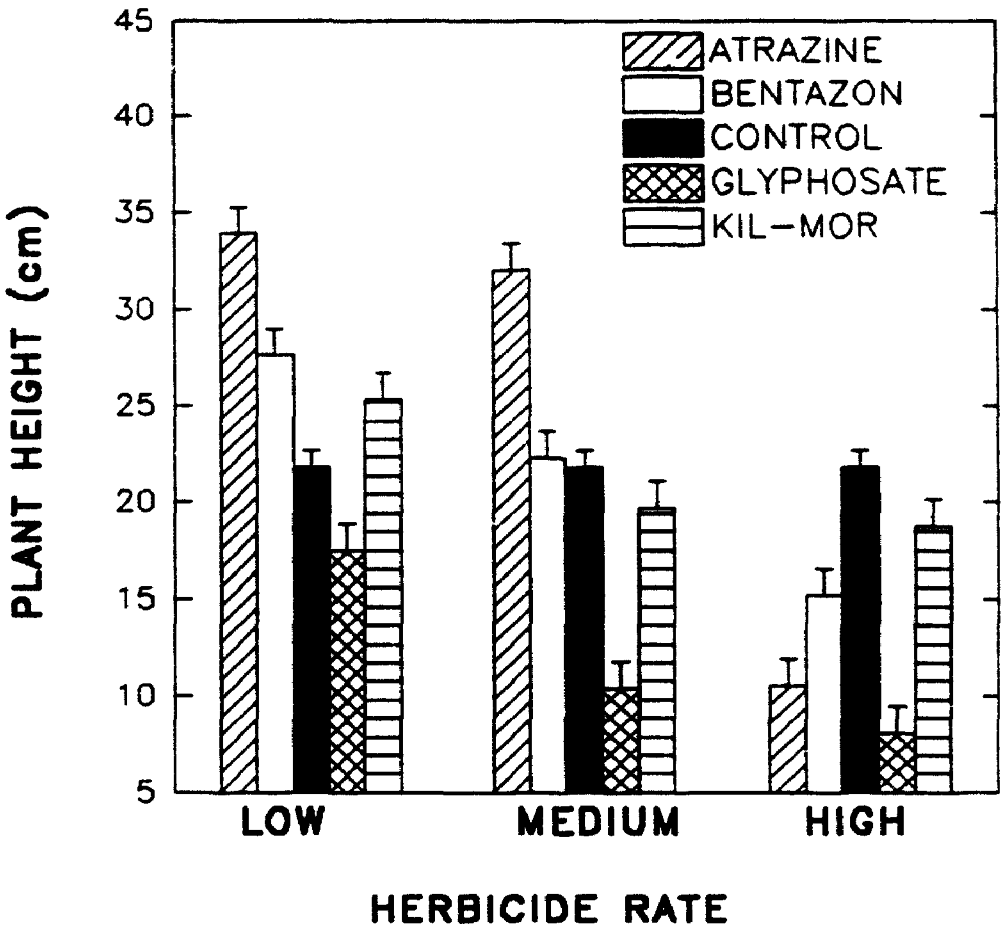
	Weight(g) per fragment	Number of buds	Days to emergence
Weight	1.000	0.161	-0.018
	0.0	0.219	0.892
Buds	0.161	1.000	-0.031
	0.219	0.0	0.815
Days	-0.0178	-0.031	1.000
	0.892	0.815	0.0

Of the paired numbers, the top number is a measure of the strength of relationship between variables and the lower one is the probability of observing a correlation coefficient as large or larger than the one obtained by chance alone (that is, when the variables in question actually have zero correlation) (Cody and Smith, 1991).

Table 13. The mean percentage survival (± S.D) of smooth ground-cherry plants four weeks after spraying with herbicides (field experiment).

Herbicide	Rate: kg ai/ha	Mean Percent survival
Glyphosate	0.623	81 (2.65)
Glyphosate	1.25	76 (6.25)
Glyphosate	2.50	60 (7.21)
Atrazine	0.56	92 (3.79)
Atrazine	1.12	89 (4.58)
Atrazine	2.24	72 (2.65)
Bentazon	0.28	90 (3.60)
Bentazon	0.56	85 (3.60)
Bentazon	1.12	87 (4.00)
Kil-Mor	0.13	90 (4.00)
Kil-Mor	0.27	88 (5.57)
Kil-Mor	0.54	90 (3.00)
Control	----	87 (4.00)

Fig. 21. The effect of four herbicides, each applied at three rates, on height (± S.E) of smooth ground-cherry 6 weeks after spraying. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25 and 2.50 kg ha^{-1}; bentazon- 0.28, 0.56 and 1.12 kg ha^{-1}; Kil-mor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with the medium and high rates for comparison. The experiment was conducted in the field.


45
40
35
30
25
20
15
10
5
PLANT HEIGHT (cm)
ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
LOW
MEDIUM
HIGH
HERBICIDE RATE

shoot branch formation (Fig. 22). The other herbicides had no significant effect on shoot branch development, irrespective of rate of application.

Glyphosate reduced leaf dry weight by 50, 60 and 73% when applied at 0.626, 1.25 and 2.50 kg ha^{-1} respectively (Fig. 23). Applications of atrazine at 2.24 kg ha^{-1} resulted in significant leaf biomass reduction, however, when atrazine was sprayed at 0.56 kg ha^{-1} it enhanced leaf biomass (Fig. 23). All Kil-Mor application rates had stimulating effects on the dry weights of leaves, stems and roots (Figs. 23, 24 and 25). Atrazine applied at 2.24 kg ha^{-1} and glyphosate at all application rates, significantly reduced stem dry weight (Fig. 24). Glyphosate applied at 1.25 and 2.50 kg ha^{-1} reduced root dry weight by 70%, whereas atrazine at 2.24 kg ha^{-1} reduced root dry weight by 80% but had no effect at the 1.12 kg ha^{-1} rate (Fig. 25). Both atrazine at 2.24 kg ha^{-1} and glyphosate at 1.25 and 2.50 kg ha^{-1} reduced the dry weight of reproductive parts (flowers + fruits) significantly, although atrazine at 0.56 and 1.12 kg ha^{-1} enhanced the dry weight of reproductive parts (Fig. 26). Neither Kil-Mor nor bentazon had significant detrimental effects on any of the plant components considered.

Fig. 22. The effects of four herbicides, each applied at three rates, on the number of branches (± S.E) per smooth ground-cherry plant. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25 and 2.50 kg ha^{-1}; bentazon- 0.28, 0.56 and 1.12 kg ha^{-1}; Kil-mor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with the medium and high rates for comparison. The experiment was conducted in the field.

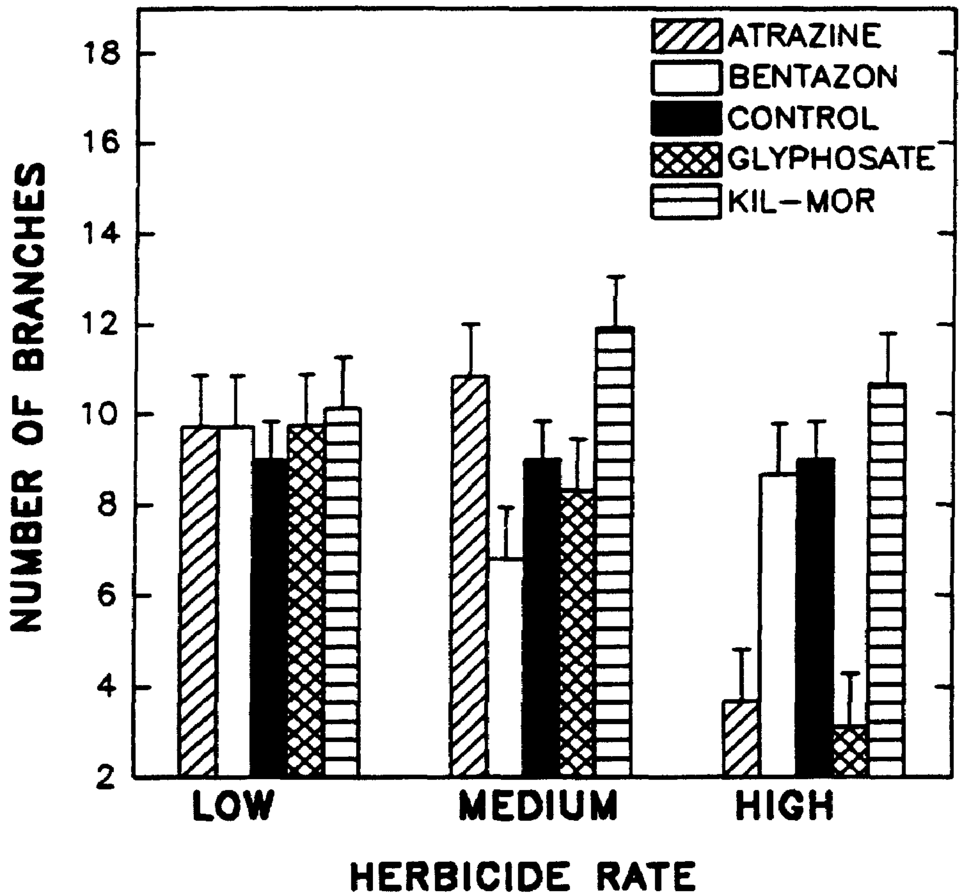
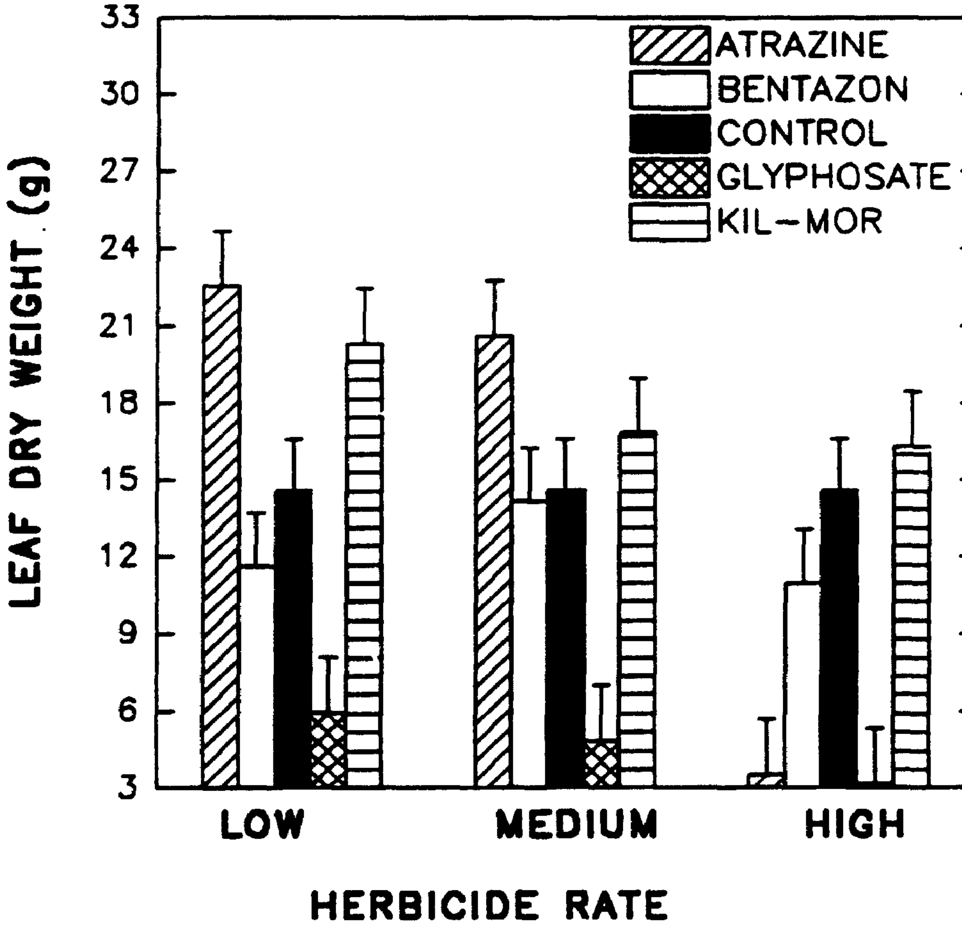

ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
NUMBER OF BRANCHES
18
16
14
12
10
8
6
4
2
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 23. The effects of four herbicides, each applied at three rates, on leaf dry weight (± S.E) of smooth ground-cherry. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25, and 2.50 kg ha^{-1}; bentazon- 0.28, 0.56 and 1.12 kg ha^{-1}; Kil-mor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with medium and high rates for comparison. The experiment was conducted in the field.



ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
LEAF DRY WEIGHT (g)
33
30
27
24
21
18
15
12
9
6
3
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 24. The effects of four herbicides, each applied at three rates, on stem dry weight (± S.E) of smooth ground-cherry. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25 and 2.50 kg ha^{-1}; bentazon- 0.28, 0.56 and 1.12 kg ha^{-1}; kil-mor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with the medium and high rates for comparison. The experiment was conducted in the field.

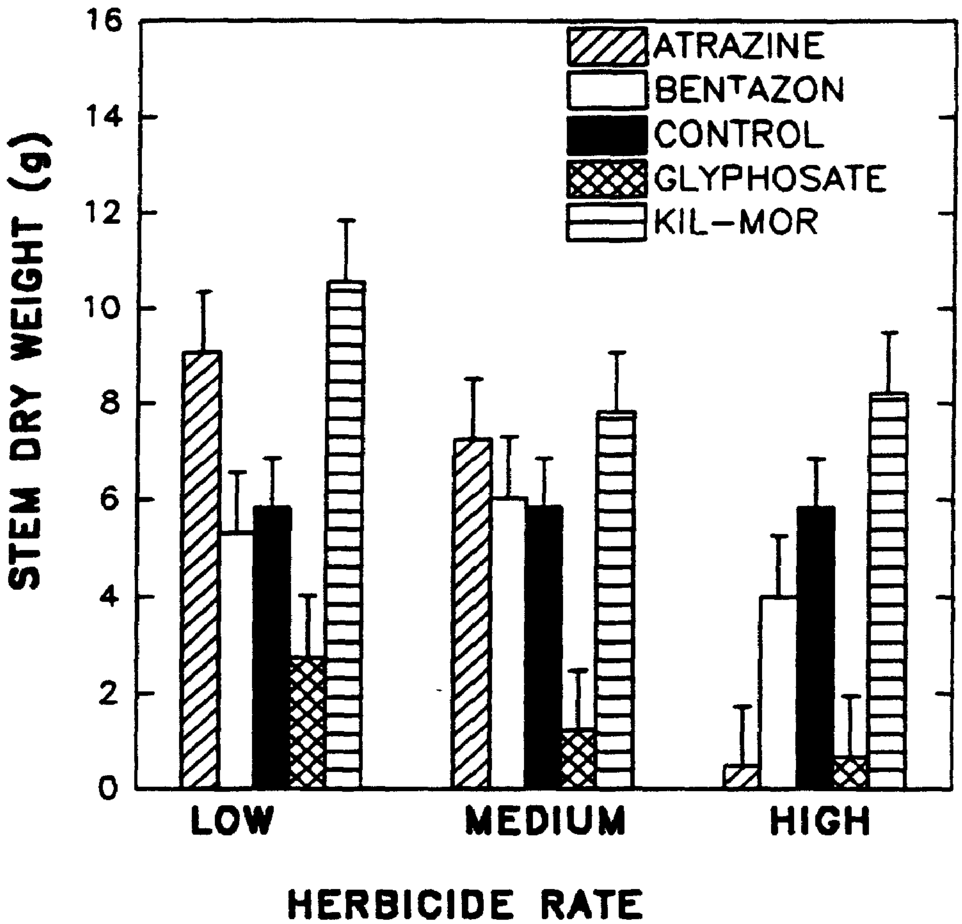

STEM DRY WEIGHT (g)
0
2
4
6
8
10
12
14
16
ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 25. The effect of four herbicides, each applied at three rates, on root dry weight (± S.E) of smooth ground-cherry. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25 and 2.50 kg ha^{-1}; bentazor - 0.28, 0.56 and 1.12 kg ha^{-1}; Kilmor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with the medium and high rates for comparison. The experiment was conducted in the field.

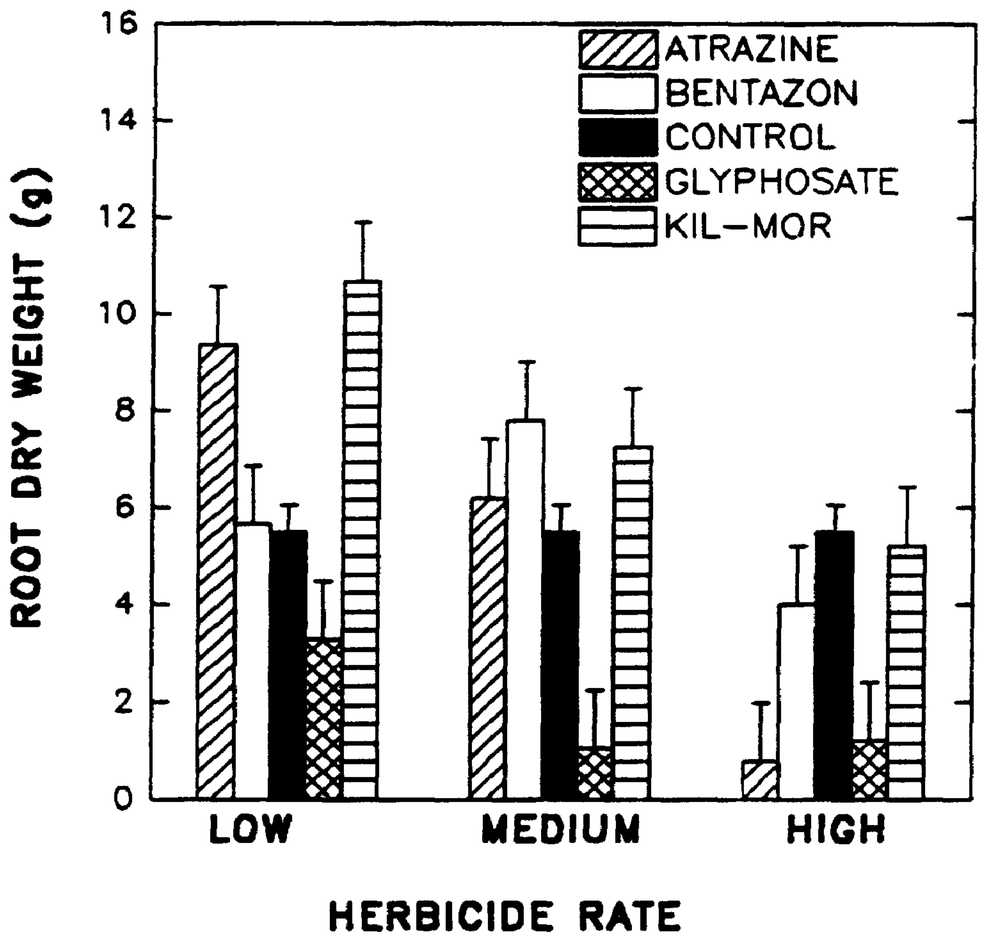
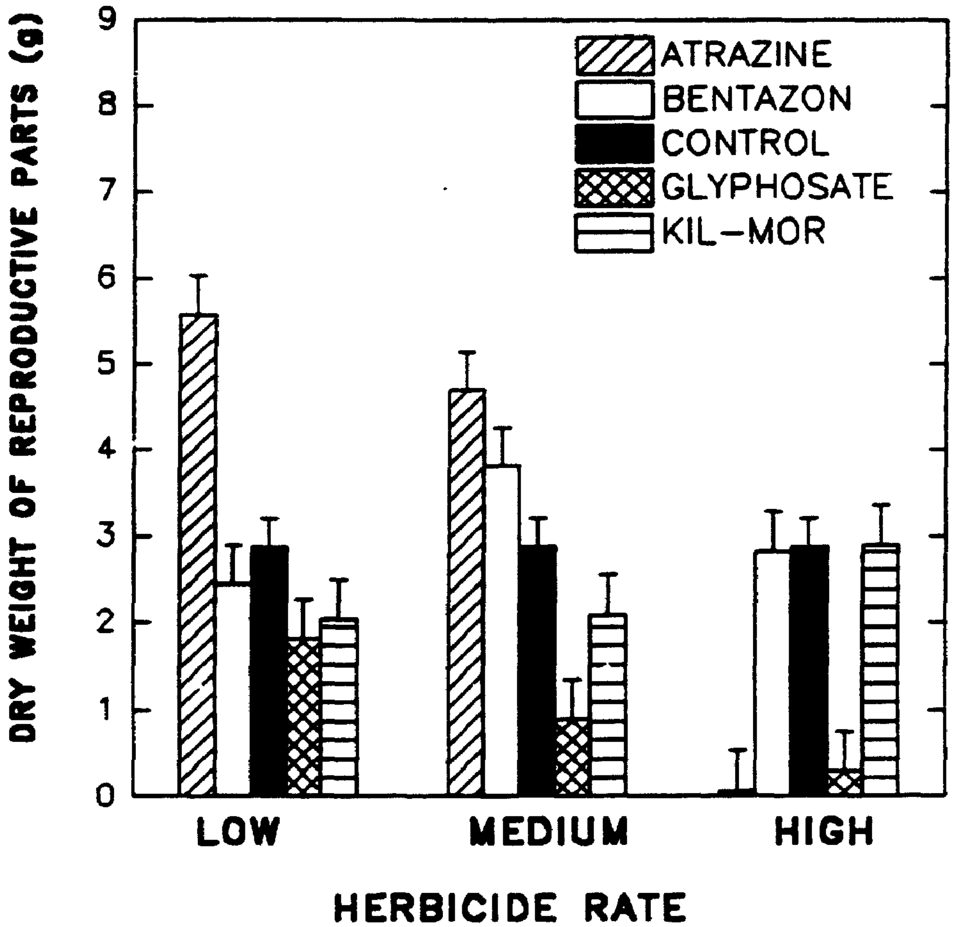

ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
ROOT DRY WEIGHT (g)
0
2
4
6
8
10
12
14
16
LOW
MEDIUM
HIGH
HERBICIDE RATE

Fig. 26. The effect of four herbicides, each applied at three rates, on dry weight of reproductive parts (± S.E) of smooth ground-cherry plants. The low, medium and high rates used for each herbicide were: atrazine- 0.56, 1.12 and 2.24 kg ha^{-1}; glyphosate- 0.63, 1.25 and 2.50 kg ha^{-1}; bentazon- 0.28, 0.56 and 1.12 kg ha^{-1}; Kil-mor- 0.14, 0.28 and 0.56 kg ha^{-1}. The control was plotted with the medium and high rates for comparison. The experiment was conducted in the field.


DRY WEIGHT OF REPRODUCTIVE PARTS (g)
0
1
2
3
4
5
6
7
8
9
ATRAZINE
BENTAZON
CONTROL
GLYPHOSATE
KIL-MOR
LOW
MEDIUM
HIGH
HERBICIDE RATE

5.4 Discussion

5.4.1 Greenhouse

The data show a remarkable tolerance of smooth ground-cherry to herbicides. Only glyphosate applied at 1.12 kg ha^{-1} resulted in total elimination of plants, whereas half of the plants treated with atrazine at 0.56 kg ha^{-1} were killed. The observed efficacy of glyphosate and atrazine could be partially attributed to the greenhouse conditions of high relative humidity, high temperatures, and abundant water supply (Thompson and Slife, 1970; Vostra et al. 1970; Casely, 1972; Chase and Appleby, 1979; Dickson et al. 1990). In general, glyphosate and atrazine were the most effective herbicides in reducing overall plant performance. Although Kil-mor reduced plant height, axillary branch development and number of flowers as effectively as atrazine, no plants were killed by Kil-mor applications. This indicates that atrazine might have disrupted vital plant life processes, e.g photosynthesis (Ashton and Crafts, 1981). On examination of the root system of plants treated with atrazine and glyphosate at the high rates, it was noted that the root system decomposed and lost much of the food reserves, leaving the vascular strands. This shows that both glyphosate and atrazine were translocated to the root system. There are no documented reports on the effects of herbicides on smooth ground-cherry, but similar effects of glyphosate and atrazine have been reported in other species (Moosavi-Nia and Dore 1979; Claus and Behrens, 1976; Wax and Behrens, 1965).

The symptoms of herbicide damage observed in this study agree with those documented for these herbicides (Ashton, 1981). Although the rate of shoot elongation (Fig. 15) in plants treated with atrazine at 0.56 and 1.12 kg/ha declined two weeks after spraying, the plants gained growth momentum four weeks after spraying at rates higher than in the control (Fig. 15). Flowers were particularly sensitive to all herbicides, however, the fourth week following treatment marked a recovery period in flower formation, except for plants treated with Kil-mor. Atrazine at 0.56 and 1.12 kg ha^{-1}, and glyphosate at 0.31 and 0.63 kg ha^{-1} reduced leaf dry weight more than they reduced stem and root dry weight. This suggests that both glyphosate and atrazine affected the plants not only through phytotoxicity (disruption of normal plant functioning through chemical means), but also by starving the roots and stems. Kil-mor and bentazon were much less effective herbicides in killing the plants, compared to glyphosate and atrazine.

5.4.2 Field station

The herbicide treatments conducted at the field station resulted in less phytotoxic effects despite a doubling of the rates used in the greenhouse. This would be expected because of lower relative humidity and temperature, less moisture availability, greater soil buffering capacity and more windy conditions (Thompson and Slife, 1970; Chase and Appleby, 1979). Furthermore, smooth ground-cherry plants in the open field could exploit more soil resources, through their deep and extensive root systems, whereas in the greenhouse the plants were pot bound. Spraying in the laboratory also delivered herbicides to the plants with greater accuracy compared to the bicycle sprayer used in the field. The symptoms of herbicide damage observed in the field were similar to those described for the greenhouse, but were milder and occurred much later . As in the greenhouse, atrazine and glyphosate were the most effective herbicides, however, unlike the greenhouse results, both herbicides were effective only at high rates. Interestingly, atrazine stimulated plant growth when applied at the low rate. Similar stimulating effects of atrazine have been reported in other species (Singh and Salunkhe, 1970; Ashton and Crafts, 1981). Plants killed by atrazine and glyphosate had soft, decomposed roots four weeks after treatment. These experiments demonstrated that smooth ground-cherry is tolerant to herbicides. Resistance has been reported in other Physalis spp. (e.g P. longifolia , Holt and Lebaron, 1990).

The sizable reduction in fruit and flower production by the high rates of glyphosate and atrazine was offset by the ability of smooth ground-cherry to regenerate vegetatively. In the next spring, most of the unharvested plants that survived the herbicide treatments resumed vigorous growth. This indicates that the root system and underground shoots did not lose their capacity to regenerate. Thus, smooth ground-cherry is well equipped to withstand repeated disturbances that may affect or completely inhibit the initiation of flowering and fruit development. Smooth ground-cherry can produce clones tolerant to chemical sprays and physical disturbances and at the same time maintain the genetic diversity of the population through seed production.

Based on the outcome of these experiments, spot treatmeants of glyphosate at about 2.2 kg ai ha^{-1} are recommended to control smooth ground-cherry infestations. Although atrazine was rather effective at the high rate of application, current Canadian regulations prohibited the use of atrazine rates above 1.5 kg ai ha^{-1} (Anonymous, 1992).

5.5 Conclusions

The overall outcome of this study shows that glyphosate and atrazine at the high rates can give satisfactory control of smooth ground-cherry plants regenerating from root pieces. This conclusion cannot be extended to established root systems of smooth ground-cherry that are producing new shoots, for the second or third years. For a herbicide to control perennial species regenerating from the root system, it must be translocated to the root. Secondary shoots that emerged three weeks after herbicide application were normal and did not show any damage. This might suggest that regrowth after application of herbicides that are translocated to the root sytem, such as glyphosate, is from dormant root buds.

In preliminary greenhouse studies, the four herbicides reported in the present investigation, were applied at the high rates to smooth ground-cherry plants at the full flowering stage. Glyphosate arrested further plant growth, and the plants remained in this arrested state for two months after which they all died. The root systems of these plants decomposed. Atrazine killed all shoots receiving treatment, but new secondary shoots emerged from buds on the root system and on the below ground stem, approximately three weeks after herbicide application. These plants were healthy and grew to large plants within six weeks of spraying. Bentazon and Kil-more treated plants had only mild injuries, which disappeared within two weeks of treatment.

It appears that smooth ground-cherry weedy populations in southwestern Ontario probably did not develop resistance to herbicides. One might speculate that it can withstand herbicide applications through:

a) limited absorption through leaves;

b)developing new shoots from dormant buds after treated shoots have died;

c)intermittent regeneration from buds on root fragments throughout most of the growing season;

d)differences in shoot sizes, in that larger early-emerging shoots act as a shield against herbicides for shorter late emerging shoots. Often these short shoots are disconnected from the root system of the bigger shoots by rotting or mechanical forces (Chapter three), hence herbicides cannot be translocated to them;

e) dilution of herbicide concentrations to non-lethal levels by the thick and fleshy root system. This will be more pronounced in plants of smooth ground-cherry regenerating from root systems older than a year;

Further investigations in the future should be directed to comparing the effects of herbicides on smooth and clammy ground-cherry populations that have never been subjected to herbicide sprays and those populations subjected to annual herbicide applications.

CHAPTER SIX

6.1 GENERAL DISCUSSION

Clammy ground-cherry and smooth ground-cherry are perennial herbs native to Canada and the United States. They grow in cultivated fields, roadsides, pastures, open woodlands, and along railway embankments. Clammy ground-cherry prefers light-textured soils with a high percentage of sand, whereas smooth ground-cherry is more commonly found in heavier-textured soils.

The two species were probably introduced into human economic activities by first invading ruderal sites, and later extended their habitat range to cultivated fields. They faced less competition in cultivated fields due to the susceptibility of competing species to herbicides. Since both species are self-incompatible they can interbreed with ruderal populations. This ensures maintanenace of genetic diversity, which can be particulary important for vegetavely regenerating species.

Both species have been described as problem weeds in Southwestern Ontario (Abdullahi, 1992). They have a remarkable capacity to regenerate from root buds, and also can reproduce by seeds. Polarity has been observed in regeneration from root fragments. Shoots mostly emerged from the proximal end of root fragments (closer to the shoot) and roots from the distal end. Polarity has been reported in other species that propagate by root cuttings (Raju et al. 1964; Cuthbertson, 1972; Hamdoun, 1972; Richardson, 1975). Earlier physiological work showed that emergence of shoots from the proximal end of root segments is due to low auxin levels in that part of the root, and that after fragmentation auxins accumulate at the distal end leading to root formation at that part of the root (Emery, 1955; Warmke and Warmke, 1950; Bonnett and Torrey, 1965).

In both clammy and smooth ground-cherry, lateral roots branched from the vertical taproot two to ten cm below the soil surface. Some of the lateral roots grew horizontally, while some grew vertically. Adventitious shoot buds were observed in seedlings five weeks after planting, and eight and nine weeks after planting, respectively, in clammy and smooth ground-cherry plants originating from root fragments. The first root buds were produced on the thicker parts of the vertical root, but later buds were being produced on horizontal laterals too. In root-derived plants buds and lateral roots were also produced from the vertical below ground stems.

In both species some horizontal laterals turned down and followed a vertical growth at about 15 to 50 cm from the main vertical root. These laterals increased in thickness starting around the bending point and below. New horizontal laterals were formed at the bending point and continued the horizontal spread. The horizontal phase of root growth was confined to the upper 30 cm of soil.

These findings are generally in agreement with those documented for other perennial herbs capable of regenerating from root buds. Frazier (1944) described the root system of Apocynum cannabinum as consisting of the original root (primary vertical) and one to many permanent lateral roots which continued to grow horizontally and on which arose roots that either grew downward directly, or did so after short horizontal growth, to become secondary vertical roots. Raju et al. (1963) classified the root system of Euphorbia esula into short roots of limited growth and no regenerative capacity, and long roots which attain considerable growth and are capable of developing new shoots from root buds. Euphorbia esula and some other species have been reported to show a root growth pattern similar to the one described here for the ground-cherries e.g. Linaria vulgaris L. (Charlton, 1966), Chondrilla juncea (Cuthbertson, 1972), Cirsium arvense (Moore, 1975), and Sonchus arvensis (Lemna and Messersmith, 1990).

Underground shoots were formed at the turning point of lateral horizontal roots, some of which emerged to become aerial shoots (satellite plants). There were no visible buds on portions of the horizontal lateral roots close to the shoot. This might be significant in spreading out the developing shoots to reduce overcrowding and competition for limited resources, and probably increases the foraging ability of the ramet. Satellite plants were not initiated until the parent shoot grew to maturity and the root system spread extensively and attained a diameter of about 6 mm. This might ensure that sufficient stored resources be available to the developing young satellite shoots until they develop enough leaf area to not only support themselves, but also contribute photosynthate to the whole ramet. In cultivated fields I observed that connections between shoots sharing the same root system dissolve during late summer through decay, thus releasing the individual shoots to independent fates.

Of the many underground shoots developed only a few emerged above the soil, thus showing establishment of correlative inhibition by the main aerial shoot. This was substantiated by noting that when the parent old shoots were clipped in stands grown for multiplication existing underground shoots grew vigourously and were capable to emerge above the soil surface. McIntyre (1979) working on Euphorbia esula, suggested that internal competition for water and nitrogen plays an important role in the mechanism of root bud inhibition. He found that the water content of the root buds increased about 25% within 24 h of the removal of the shoot of the parent plant and that subsequently root bud length increased significantly.

In general, root-originating clammy ground-cherry plants had higher productivity than either smooth ground-cherry plants or seed-originating clammy ground-cherry plants. A vegetatively regenerated plant starts with a larger capital than a seedling, which may account for the relatively higher vigour of the former.

Most of the weedy populations of these two species regenerate from root buds and seedlings seem to be less important. In many perennial species that regenerate vegetatively, seeds were reported to play minor roles in population establishment (e.g. Cirsium arvense (Donald, 1992), Elytrigia repens (Majek et. al, 1984) Sparganium eurycarpum (Leif and Oelke, 1990)).

The formation of long horizontal roots loaded with buds and underground shoots during a season in the two species, allows them to raise and support several aerial shoots during the next growing season, until these shoots develop enough photosynthesizing leaf surface to be independent. In most clonal plants that have been studied, movement of resources is from old ramets to young ramets (Pitelka and Ashmun, 1985). Plants that arise from seed and do not spread vegetatively must exploit the immediate soil environment regardless of its quality (Harnett and Bazzaz, 1985). Clonal plants, on the other hand, when spreading into new soil environments, are receiving resources translocated from ramets in different soil environments. This also leads to rapid growth early in the season. For example, in corn fields, clammy ground-cherry flowered when the corn was still at the seedling stage (Abdullahi, unpublished).

The results indicated that both species are capable of regenerating from root fragments as short as 2.5 cm long and can send up shoots from at least 15 cm deep. The probability of emergence was higher with longer fragments and with shallower depths of burial. Similar results were noted in other species (*Cirsium arvense*, Hamdoun, 1972; *Chondrilla juncea*, Cuthbertson, 1972; *Saponaria officinalis*, Lubke and Cavers, 1970). However, root fragments left at the soil surface did not survive, because of desiccation. This implies that root fragments brought up to the soil surface by tillage equipment will not contribute to new ground-cherry establishment. The orientation of the root fragments in the soil at planting had no effect on their subsequent capacity to develop shoots in either species. Mann and Cavers (1979) observed reduced regenerative capacity in root fragments of *Taraxacum officinale* planted in orientations other than the normal vertical direction. However, this species lacks the horizontally spreading thick roots common in many perennial herbs including the ground-cherries. The absence of orientation effects in the ground-cherries could have survival value under periodically tilled agricultural soils.

In both species significantly fewer root fragments sampled from plants at the fruit dispersal stage regenerated compared to those obtained in the early vegetative stage. In the field root fragments sampled from plants dispersing fruits (October) failed to regenerate. When excavated in May, 1993, these fragments were firm and had initiated new root buds. The reduced fragment regeneration and the prolonged time to shoot emergence observed in the greenhouse during the last sampling (October) might indicate onset of dormancy. The ecological significance of root bud dormancy is the ability to avoid the commitment of resources to new growth in a season when the probability of life cycle completion is very low.

Although more than 90% of the root fragments with visible buds regenerated in both species regardless of their original position in the root system, less than half of those without visible buds regenerated. Root fragments as thin as 1.5 mm regenerated almost completely if they had visible buds at planting, and about 40% regenerated if they had no visible buds. The lack of regenerative capacity of root fragments less than 1.5 mm in thickness indicates that control by cultivation can be successful with plants developing from seedlings. Cuthbertson (1972) reported that in Chondrilla juncea root cuttings from all depths exhibited a marked regenerative capacity. Raju et al. (1964) found that root fragments of Euphorbia esula from all depths up to 280 cm, regardless of the presence or absence of preformed buds, had an extensive regenerative capacity.

Smooth ground-cherry showed a remarkable tolerance to herbicides. In both greenhouse and field experiments, bentazon and Kil-Mor were less effective than glyphosate and atrazine. Plants killed by the application of glyphosate and atrazine at a time of vigourous growth had soft, decomposed roots , suggesting that these herbicides had been translocated to the root system. Low rates of atrazine and Kil-mor applications in the field had stimulating effects on growth of smooth ground-cherry plants. In the field study, secondary shoots that developed three weeks after herbicide application were normal and had no symptoms of injury. These shoots probably were from buds that were dormant at the time of herbicide application. Bud dormancy is the main source of difficulty in killing perennial weeds (Aldrich, 1984). Roots fail to translocate herbicides to inactive root buds and thus these buds can be the source of new growth. Spot treatments of glyphosate at 2.2 kg ai ha^{-1} applied to actively growing plants, can be recommended to control smooth ground-cherry infestations. It is likely that stands of smooth ground-cherry older than a year will show greater tolerance to herbicides than those recently establishing from root fragments, because of the greater and deeper root biomass with a capacity to dilute herbicides to non-lethal concentrations. In established stands, especially under no-till environments, biomass is added annually to the same root system, so that it can accumulate a massive root reserve over time. Smooth ground-cherry probably did not develop resistance to herbicides, but might withstand herbicide treatments through: limited absorption through leaves; development of new shoots from dormant buds; intermittent regeneration from root buds; severing connections between shoots through root decay; differences in shoot size; and dilution of herbicides by massive root tissue.

The present investigations have showed that clammy and smooth ground-cherry can survive in highly disturbed agricultural habitats through their capacity to develop horizontally spreading and deeply-penetrating thick roots rich in reserves, their capacity to raise shoots from buds located in these roots, their ability to regenerate from root fragments of almost any length, their ability to regenerate from all depths within the plough zone, their capacity to not only survive harsh winter conditions by an extensive intact root systems but also as root fragments, their capacity to resist decay after fragmentation, their ability to propagate from almost any part of the root system through intermittent shoot development, their development of dormancy late in the growing season, and their tolerance of commonly used herbicides.

Further research in the future should address competition of the two ground-cherry species with crops, e.g corn or soybeans and the effects of herbicides not only on weedy populations subjected to annual herbicide applications but also on natural populations.

Appendix 1. Summary of Anova for seasonal growth of clammy and smooth ground-cherries.

	Height	Root length	Leaf Area	Root dry weight	Shoot dry weight	Number of Unsh.[#]
Source	pr>F	pr>F	pr>F	pr>F	pr>F	pr>F
Block	0.005	0.751	0.032	0.409	0.169	0.0300
Species	0.826	0.0001	0.0001	0.0001	0.0001	0.0001
Origin	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Harvest	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Species x origin	0.739	0.0001	0.0001	0.0001	0.0001	0.0001
Species x harvest	0.663	0.0001	0.0001	0.0001	0.0001	0.0001
Origin x harvest	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Species x origin x harvest	0.083	0.0007	0.0001	0.0001	0.0001	0.0001

Unsh. = Underground shoots

Appendix 2. Summary of Anova for the effects of root fragment size and depth of fragment burial on clammy and smooth ground-cherries.

	Shoot dry weight	Height
	Fragment size	
Source	pr>F	pr>F
Species	0.411	0.072
fragment size	0.206	0.126
Species x size	0.397	0.286
	Depth of fragment burial	
Source	pr>F	pr>F
Species	0.002	0.681
Depth	0.223	0.512
Species x depth	0.438	0.933

Appendix 3. Summary of Anova for the effects of root fragment orientation on clammy and smooth ground-cherries.

	Days to emergence	Number of shoots
	Field experiment	
Source	pr>F	
Species	0.001	
Orientation	0.055	
Species x orientation	0.278	
	Greenhouse experiment	
Source	pr>F	pr>F
Species	0.001	0.0001
Orientation	0.079	0.610
Species x orientation	0.054	0.349

Appendix 4. Summary of Anova for the effects of growth stage on the capacity of root fragments of clammy and smooth ground-cherries to regenerate.

	Days to emergence	Number of shoots
	Greenhouse experiment	
Source	pr>F	pr>F
Species	0.0001	0.167
Growth stage	0.0001	0.198
Species x growth stage	0.093	0.062
	Field experiment	
Source	pr>F	
Species	0.015	
Growth stage	0.0001	
Species x growth stage	0.001	

Appendix 5. Summary of Anova for the effects of origin of root fragments of clammy and smooth ground-cherries on their subsequent capacity to regenerate.

	Days to emergence	Number of shoots
<u>Source</u>	<u>pr>F</u>	<u>pr>F</u>
Species	0.009	0.272
Origin	0.001	0.081
Species x origin	0.056	0.887

Appendix 6. Root fragment fresh weight, number of buds per root fragment (before planting), and days to emergence of smooth ground-cherry (greenhouse study).

Fragment number	Fresh weight (g)	Number of buds	Days to emergence
1	3.04	10	5
2	6.55	4	8
3	3.01	12	8
4	11.21	5	5
5	4.80	9	5
6	4.66	4	5
7	4.15	9	8
8	3.33	2	8
9	7.33	12	5
10	5.86	32	5
11	12.12	17	6
12	8.08	26	5
13	3.04	5	5
14	3.74	14	5
15	7.55	3	5
16	5.53	22	5
17	6.53	13	5
18	6.37	2	8
19	5.76	1	5
20	4.92	12	11
21	4.58	27	5
22	5.93	3	5
23	9.92	11	8
24	3.70	5	5
25	6.30	2	6
26	4.56	8	8
27	5.36	3	9
28	4.28	19	6
29	7.02	29	6
30	11.01	5	5
31	7.07	4	8
32	9.78	23	5
33	7.81	6	5
34	7.67	3	5
35	8.71	10	6
36	5.38	2	6
37	4.24	1	6
38	5.23	5	8
39	8.72	3	5
40	6.37	33	10
41	9.86	16	6
42	5.54	4	6
43	8.90	12	5
44	4.42	25	5
45	8.16	10	5
46	4.72	19	9

Appendix 6 continued:

Fragment number	Fresh weight (g)	Number of buds	Days to emergence
47	7.46	15	5
48	5.67	11	5
49	7.82	2	5
50	6.50	13	5
51	7.31	23	6
52	12.20	8	6
53	9.40	3	6
54	5.13	27	9
55	6.58	17	8
56	5.73	10	6
57	11.33	3	6
58	3.43	28	5
59	6.57	9	6
60	8.85	20	6
61	5.19	3	6
62	3.23	4	6
63	5.19	6	6
64	3.94	18	6
65	3.30	11	8
66	4.00	14	7
67	3.13	5	8
68	5.98	10	5
69	7.76	11	8
70	7.54	2	6
71	5.16	7	10
72	5.19	2	10
73	4.26	3	10
74	4.72	12	7
75	4.40	5	8
76	5.13	17	6
77	4.05	21	5
78	4.47	9	8

Appendix 7. Summary of Anova for the effects of herbicides on smooth ground-cherry.

	Height	Number of branches	Number of flowers	Stem dry weight	Leaf dry weight	Root dry weight	dry weight reprod. parts
			Greenhouse experiment				
Source	pr>F	pr>F	pr>F	pr>F	pr>F	pr>F	
Herb	0.0001	0.0004	0.0001	0.001	0.0001	0.0007	
Rate	0.074	0.626	0.055	0.096	0.001	0.002	
Herb x rate	0.012	0.0636	0.077	0.0004	0.037	0.012	
Herb x week	0.0001	0.0001	0.0001				
			Field experiment				
Source	pr>F	pr>F		pr>F	pr>F	pr>F	pr>F
Herb	0.0001	0.004		0.0001	0.0001	0.0001	0.0001
Rate	0.0001	0.0008		0.003	0.0001	0.0001	0.0001
Block	0.922	0.338		0.418	0.228	0.056	0.015
Herb x rate	0.0001	0.005		0.005	0.0001	0.001	0.0001

Appendix 8. Root fragment fresh weight, number of buds per root fragment (before planting), and days to emergence of smooth ground-cherry (Field experiment).

Fragment number	Fresh weight (g)	Number of buds	Days to emergence
1	2.47	11	23
2	5.88	9	28
3	1.95	3	22
4	10.78	7	30
5	4.94	24	20
6	9.96	2	31
7	5.84	5	21
8	10.42	18	20
9	2.55	13	21
10	2.29	9	22
11	9.37	16	23
12	4.33	10	25
13	1.50	2	26
14	2.25	3	29
15	2.90	7	31
16	4.91	27	33
17	3.10	4	30
18	3.62	11	23
19	4.55	5	22
20	3.60	9	24
21	4.20	19	27
22	5.85	10	28
23	2.59	14	31
24	7.20	11	26
25	2.62	2	33
26	5.63	15	23
27	6.77	23	19
28	7.93	8	25
29	3.16	4	22
30	7.31	25	20
31	5.16	16	21
32	3.12	9	24
33	2.27	5	27
34	1.98	27	30
35	6.20	7	26
36	3.59	11	22
37	8.35	19	27
38	2.98	3	20
39	4.25	8	22
40	2.92	6	25
41	10.97	5	31
42	2.56	10	30
43	2.26	4	18
44	5.43	17	23
45	2.38	13	20
46	3.13	6	21

Appendix 8 continued:

Fragment number	Fresh weight (g)	Number of buds	Days to emergence
47	2.70	18	20
48	3.55	9	24
49	3.45	21	28
50	2.94	3	26
51	6.50	14	25
52	14.54	7	20
53	7.93	18	22
54	3.62	5	21
55	1.86	4	24
56	4.10	2	27
57	2.61	9	31
56	5.35	17	35
57	2.61	6	19
58	5.35	21	23
59	8.05	5	21
60	7.81	19	25

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