AUTECOLOGICAL AND GRAZING CONTROL STUDIES OF DYERS WOAD (*ISATIS TINCTORIA* L.) ON NORTHERN UTAH RANGELANDS

by

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DEDICATION

To my Grandfather, SHEIKH FARAH, who has opened the gates of knowledge to generations yet unborn.

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Kassim O. Farah

TABLE OF CONTENTS

TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

ABSTRACT

Autecological and Grazing Control Studies of Dyers Woad (*Isatis tinctoria* L.) on Northern Utah Rangelands

by

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Dyers woad (*Isatis tinctoria* L.) is a noxious weed on northern Utah rangelands. Chemical and mechanical means of control are unsuitable for rangelands. A potential alternative, biological control, is difficult due to a lack of basic ecological information. To remedy this, some aspects of the population biology and autecology of dyers woad were studied. The feasibility of controlling dyers woad by early spring grazing was also investigated via clipping experiments.

A population study followed the survivorship of experimentally established populations over two years. Fall germinating individuals (1984) overwintered as rosettes twice and all survivors reproduced successfully. Spring germinating individuals (1985) overwintered as rosettes only once and 87% seeded the subsequent spring. Thus, on a good condition (high seral) foothill rangeland, dyers woad behaved predominantly as a biennial. Peak mortality in both fall and spring populations coincided with summer drought. The population size of dyers woad was constricted at two stages: (i) germination and establishment, and (ii) young rosette. The risk of mortality

mortality in young rosettes was 77%. Dyers woad should be targeted for biological control at this vulnerable stage of growth.

The seed dispersal pattern of dyers woad was best described by a negative exponential model of the type $\log y = a + bx$; ($r = .78$, $a = 1.92$, and $b = -0.02$). Ninety-five percent of all fruits were deposited within 54cm of mother plants. The root system of dyers woad was predominantly a taproot with some laterals in the upper 30cm of the soil. There was little difference between mapped taproot and total mapped root lengths of rosette and mature plants.

Significant mortality and reduction in reproductive performance occurred only by clipping, on or after 23 May 1984, at 60% or 90% intensity. Clipping twice, at either intensity, before 23 May had no effect on dyers woad. Sheep utilization of dyers woad ceased after mid-May, and had no significant effect on its mortality, percent flowering, and fruit production. Sheep grazing on dyers woad did not occur when much impact on mortality or seed production could be expected. The stocking required to restrict dyers woad will result in range deterioration. More host-specific biological control agents should be tried.

(126 pages)

CHAPTER I

INTRODUCTION

Dyers woad (Isatis tinctoria L.), a member of the mustard family, is an aggressive weed that has been rapidly spreading in croplands and rangelands of northern Utah and surrounding states. Chemical and mechanical controls have been developed for croplands. However, due to destruction of non-target, desirable forage plants, steepness and rockiness of most range sites, and questionable economic returns, these methods are unsuitable for most rangelands. A potential alternative is biological control, a method rendered difficult due to a paucity of basic ecological information on dyers woad. Despite the lack of this information, observation by graziers suggests that where early spring grazing by livestock had taken place, there are apparently less dense populations of dyers woad. This raises the possibility of approaching dyers woad control by biological means through livestock grazing.

This research attempts to further the understanding of possible grazing control of dyers woad on northern Utah rangelands in two respects: (i) elucidate some autecological features of dyers woad that are likely to assist in its control, and (ii) determine combinations of intensity, frequency and timing of simulated grazing that causes significant mortality, and reduction in flowering and seed production of dyers woad. Autecological investigations included description of seed dispersal pattern, rooting patterns, and survivorship trends of experimentally established populations.

Objectives

The specific objectives of this study were to:

1. Describe the survivorship trends of experimentally established populations of dyers woad over a two year period.
2. Determine the life cycle of dyers woad under natural rangeland conditions.
3. Describe patterns of dyers woad seed dispersal by wind.
4. Determine the depth and pattern of spread of the roots of dyers woad.
5. Determine the combined effect of intensity and frequency of clipping on the mortality, percent flowering, and seed production of dyers woad.
6. Determine the effect of time of clipping (with respect to seasonal progression) on the mortality, percent flowering, and seed production of dyers woad.
7. Assess the degree of utilization of dyers woad by sheep in a grazed pasture over a growing period.
8. Determine the effect of sheep grazing on the mortality, percent flowering, and seed production of dyers woad.

Hypotheses

Objectives 1, 2, 4, and 7 are largely descriptive whereas the others lead to the following testable hypotheses:

Hypothesis 1: Seed dispersal pattern of dyers woad around a mother plant will not conform to a negative exponential model.

Hypothesis 2: Clipping, at several combinations of intensity and frequency, will have no effect on the mortality, percent flowering, and seed production of dyers woad.

Hypothesis 3: There will be no difference in mortality, percent flowering, and seed production between dyers woad plants clipped earlier and those clipped later in the growing season.

Hypothesis 4: Sheep grazing will have no effect on the mortality, percent flowering, and seed production of dyers woad.

CHAPTER II

REVIEW OF LITERATURE

Dyers Woad

Dyers woad (Isatis tinctoria L.) belongs to the Brassicaceae or mustard family. It may be a winter annual, biennial or short-lived perennial (Hurry 1930, Gilkey 1957, King 1966, 1967, Varga and Evans 1978). Germination and vegetative growth occur both in the fall and spring. Root development and rosette formation occur during the first growing season. During the second year, the rosettes "bolt", forming erect stems which produce yellow flowers borne on short racemes (Hurry 1930, Varga and Evans 1978). In 1983, plants flowered during early May while seed set was completed by early June at foothill rangeland sites in northern Utah (Fuller 1985). In southeastern Idaho, time of peak bloom for dyers woad was correlated with elevation (probably as a function of temperature). It ranged from 23 May to 7 June in 1983, depending on altitude (Callihan et al. 1984). On occasion, crown buds on plants that have flowered will survive, allowing plants to persist for three or more seasons (Callihan et al. 1984). Dyers woad has two dormancy periods: during summer and again during winter (Fuller 1985).

Dyers woad possesses two distinct morphological forms: (1) a vegetative form consisting of rosettes, and (2) a reproductive form comprised of flowering stalks in addition to the basal rosette (King 1966, Fuller 1985). The rosette leaves are bluish-green, slightly pubescent and have distinct white midveins (Varga and Evans 1978, Callihan et al. 1984). Rosette diameter usually ranges between 3.5 and

18cm. Basal leaves are elliptic and succulent (Welsh and Reveal 1977). The stem leaves are sessile and sagittate (Hurry 1930). The flowering stalks, which may be single or multiple, range between 30 and 150cm in height (Hurry 1930, Varga and Evans 1978, Callihan et al. 1984). The inflorescence consists of several racemose branches arranged in corymbose panicles. Both sepals and petals are yellow and are commonly visited by bees. Dyers woad has, however, the capacity to self-pollinate (Hurry 1930). Fruits of dyers woad are pendulous, winged, single seeded, and indehiscent. The fruits are glabrous and green, turning dark brown to purplish when ripe. Fruit size varies between 10 to 18mm in length and 5 to 9mm in width (Hurry 1930, Welsh and Reveal 1977, Varga and Evans 1978, Callihan et al. 1984). There are no known reports of fruit weights of dyers woad.

Dyers woad is considered a native of southeastern USSR (Hurry 1930, King 1966, 1967) but currently occurs in Asia, North Africa, Europe, North and South America, and Australia. Around the 13th century and as recent as 1900, dyers woad was cultivated in Europe for the blue dye, indigotine, extracted from its leaves. This substance was eventually replaced by indigo and artificial dyes (Hurry 1930, King 1967, Varga and Evans 1978). The woad plant also has been widely used in medical and surgical therapeutics (Hurry 1930, King 1967).

In the U.S.A., dyers woad is found in West Virginia and surrounding states where it was first cultivated for its blue dye or as an ornamental during the colonial period. (Corbett 1973, Varga and Evans 1978, King and Evans 1983). Alfalfa seeds contaminated with dyers woad seeds, imported into Siskiyou County, California from Ireland in the early 1900's, are believed to be the source of the present populations of dyers woad in northern California and southern Oregon (Young and Evans 1977). An introduction near Brigham City, Utah (about 1910), probably also from contaminated alfalfa seed, is responsible for the current, dense populations in northern Utah, southeastern Idaho, and western Wyoming (King 1967).

In the past few decades, dyers woad has officially entered the ranks of noxious weeds in northern Utah (Varga and Evans 1978) and southeastern Idaho (Callihan et al. 1984). Dyers woad has become an aggressive weed and occurs in dense infestations that substantially reduce forage production (Young and Evans 1977, Evans and Chase 1981). The ways in which dyers woad colonizes and dominates are not clear, but probably include allelopathic properties of fruits, prolific seed production (Young and Evans 1971) and rapid growth rates (Callihan et al. 1984).

Dyers woad can be controlled mechanically or by herbicides. The plant can be destroyed by digging, hoeing or plowing during the first year of growth (Varga and Evans 1978, Evans and Chase 1981). These investigators have also shown that 2,4-D at a rate of 1.5 Lb/A, is effective on rangelands, if repeated and followed by rogueing. Application of this herbicide after plants have started to set seed is not only ineffective, but is likely to reduce the land's overall productivity (Varga and Evans 1978). Recently, King and Evans (1983) reported lowered seed production and seed pod formation when woad plants were treated during the late flowering stage with a mixture of chlorsulfuron and DPX-T6367.

Population Biology and Weed Control

A primary aim of population biology is to enhance the understanding of how and why populations change (Silvertown 1982). This discipline entails comprehension of processes that regulate the size and composition of populations and the causes of establishment, growth and decline (Sagar and Mortimer 1976, Ter Borg 1979). Population biology deals with the life cycle of organisms, without which the description of a population is inadequate. This discipline also attempts to discern the direct effects of the physical environment and the influence of biotic stress attending the growth of populations (Harper 1977).

Demography is a component of population biology that has historically been restricted to descriptive aspects of population fluctuations. It may be defined as the science of vital statistics of births, deaths, reproductive rates, and age of individuals in populations (Barbour et al. 1980). Demography has classically been the province of zoologists (Harper 1984) and constituted the framework for studies on mechanisms of population regulation. In recent years, however, demographic techniques have been used by plant ecologists to assist in biological control of weedy species (Sarukhan 1974, Mortimer 1983).

Detailed population studies may provide insight into how populations of weedy species are regulated. Such studies also help expose weak points in the sequence of demographic events during which control of populations is likely to be effective (Cussans 1974, Sarukhan 1974). Questions of how and when weed populations are regulated should be answered. To achieve this goal, quantitative information about the size and dynamics of populations must be accumulated over an appropriate period of time. If such data are related to the relevant unit of the population (e.g., genets and/or ramets) and detailed life-tables are constructed, it is possible to identify phases when control may be best effected (Harper 1967, Sagar 1970, Cussans 1974).

Demographic studies also yield information that allows computation of the magnitude of reduction in reproductive output required to prevent increase in population size. Lashley 1969 (*In*: Sagar 1974) found that 98% seed loss was required to control populations of *Carduus nutans*. Consequently, studies of mortality and fecundity in natural populations should be beneficial in devising weed control strategies. For example, Cussans (1968) recorded loss of seed of *Avena fatua* in excess of 95%, of which a very high proportion occurred in the initial 3-4 months after shedding from the parent plant. Identifying and quantifying the relative proportions of sources of mortality can be largely achieved via demographic studies (Sagar 1974). Several investigators have employed demographic approaches to understand population fluxes in weeds (Putwain 1970, Sagar 1970, Sarukhan 1974, Sagar and Mortimer 1976).

Survivorship Trends in Populations of Herbaceous Plants

Patterns of mortality observed in plant populations can be correlated with two factors: (i) life cycle and life form of the species, and (ii) prevailing circumstances in the different habitats which populations occupy (Silvertown 1982).

Ecologists wishing to explain correlations between habitat, abundance, and distribution of species have stressed the critical role of the seed and/or seedling environment in determining the subsequent dynamics of adult populations (Sagar and Harper 1961, Harper and White 1974, Grubb 1977). Sagar (1970) reported that for Plantago lanceolata, constriction of population size occurred at most stages of the life cycle, with substantial loss through germination failure and mortality of seedlings. Palmblad (1968) concluded that controlled germination, and mortality at various stages, were major constraints to population growth in several annual and perennial weedy species.

Demographic approaches to studies of plant populations have received attention only recently. Harper and White (1974) reviewed studies of survivorship of Ranunculus spp. (Sarukhan and Harper 1973); Anthoxanthum odoratum (Antonovics 1972); and a number of other perennial herbs. Actuarial data have also been used to provide information required for modelling population growth (Sarukhan and Gadgil 1974, Werner and Caswell 1977, Begon and Mortimer 1981).

Several studies of survivorship described low juvenile mortality for annual species (Baskin and Baskin 1972, 1974, Leverich and Levin 1979, Jeffries et al. 1981). A contrasting observation was made by Sharitz and McCormick (1973) who found high juvenile mortality for Minuarta uniflora. This annual species grows on rock outcrops where the seedlings can easily be washed away by rain. In a study of the sand dune annual Cerastium atrovirens, Mack (1976) determined that the probability of a seedling becoming a reproductive individual was low. However, those individuals that survived to maturity possessed high reproductive output. Watkinson (1978) found an opposite situation for the annual dune grass Vulpia fasciculata. Beatley (1967), investigating a variety of autumn germinating winter annuals of Mojave Desert, found that mortality ranged between 37 and 90% during one growing season. Klemow and Raynal (1981) reported that survivorship patterns of Melilotus alba varied depending on date of emergence, temperature, and rainfall during the first year of growth. They found that under relatively cool and moist conditions, survivorship was exponential (constant mortality), while during hot dry years, the survivorship trend was concave (high juvenile mortality).

Sarukhan and Harper (1973), in a detailed study of the demography of three buttercups, (Ranunculus bulbosus; R. repens; and R. acris), concluded that seedlings suffered a very high risk of mortality relative to mature plants. West et al. (1979) reported that survivorship fluxes of a variety of perennial plants in a semi-arid environment, including Agropyron spicatum, Oryzopsis hymenoides, and Stipa comata, among others, could not be fitted by a single model. The appropriate model changed with the age class considered. Overall, it appears difficult to generalize on survivorship patterns of annuals and short-lived perennials (Ter Borg 1979).

Dispersal of Seeds

Attempts to understand the distribution of a plant species over its range of habitats and the dynamics of its populations must include the process of seed dispersal. Seed dispersal is important in the dynamics of a population in two respects: (i) that of augmenting or depleting local populations, thus altering population size, and (ii) expansion of the range of habitat occupied by a species, i.e., the founder effect (Harper 1977, Silvertown 1982).

The probability of a seed falling on a unit area of land might depend on several variables: (i) the height and distance of the seed source (ii) the number of seeds at the source (iii) dispersal characteristics of the seed, e.g., its weight, presence of wings etc., and (iv) activity of dispersal agents e.g., wind speed and wind direction (Cremer 1965, Burrows 1973, Harper 1977). Seeds dispersed by wind, whether facilitated by dispersal appendages (e.g., wings) or not, do not generally move very far from mother plants (Sheldon and Burrows 1973, Ter Borg 1979, Marchand and Roach 1980). In the case of wind dispersal, a functional relationship may be expected to exist between seed density at a given location and distance from source. Harper (1977) evaluated patterns of dispersal for eleven plant species and hypothesized that, in general, dispersal tended to decline with increasing distance from the source and that these patterns could be quantitatively described by a negative exponential model.

Most of the data to support the negative exponential model comes from studies of weedy species and forest trees. Studies on both kinds of plants were conducted either on isolated individuals or from the edge of dense stands (Harper 1977). The dispersal of seeds within a more or less continuous population is difficult to study because seeds have to be labelled to distinguish them from those of the same species in neighboring areas. Radioactive tracers (Colwell 1951, Lawrence and Rediske 1962, Watkinson 1978), flourescent dyes and paints (Naylor

1972, Werner 1975a, Mortimer *In*: Harper 1977, Watkinson 1978) have successfully been used to mark individual seeds and follow their fate.

The relationship between seed number and distance from a stand of *Senecio jacobaea* was studied by Poole and Cairns (1940) in a New Zealand pasture. These investigators found that of all seeds shed, 60% were deposited around the base of the plants while 39% were distributed further than 4.6m from the edge of the plants; only .005% were distributed more than 36m. Bakker (1960), in a study of dispersal of seeds of *Tussilago farfara* over a much greater distance (> 4 km), found a similar type of distribution around seed sources.

Yocom (1968) demonstrated that, of the total seeds of short leaf pine (*Pinus echinata*) trapped in 1963 and 1964, 50% fell less than 20m from the forest edges while 85% fell within 50m. Roe (1967), studying seed dispersal of Englemann spruce (*Picea engelmannii*) in a forest clearing, found a strikingly regular relationship between the logarithm of the seed deposited and the distance from the forest edge. Boyer (1958), working with long leaf pine (*Pinus palustris*), reported that 66% of all viable seeds trapped fell under the forest canopy and 23% were dropped within 20m of the forest edge. He contended that seed dispersal of this species generally followed a negative exponential model.

Werner (1975a), investigating teasel (*Dipsacus fullonum*), concluded that seed deposition around mother plants was related to distance, and dispersal of seeds for this species followed a negative exponential function. Watkinson (1978), studying *Vulpia fasciculata* (a winter annual grass in Britain), demonstrated that distribution of dispersal units (caryopses) around parent plants was in accordance with Werner's (1975a) negative exponential model.

Rooting Studies

The fraction of soil moisture and nutrients extracted by an individual plant is largely dependent on the depth, density, and relative activity per root length of its rooting system (Nye and Tinker 1977, Fitter and Hay 1981). The timing and pattern of root growth culminating in a given root form is largely controlled by the spatial and temporal variability in moisture and macronutrients in the soil profile, though genetic factors have some role (Richards 1986).

Root growth is important in determining the competitive ability of plants (Weaver 1958, Davies et al. 1965). Although Pavlychenko (1937:62) stated that "competition commences under the soil surface when root systems overlap", it is now known that belowground competition for resources starts as soon as their depletion zones overlap (Fitter and Hay 1981). Deep-rooted plants generally survive drought better than shallow-rooted ones because more water is accessible to deep-rooted systems. However, shallow rooted plants may intercept surface moisture to the exclusion of the deep-rooted types (Kramer 1969).

Belowground interference between plants has received little research attention. The main reasons that little field root research has been conducted are attributed to methodological difficulties. Bohm (1979), reviewing methods of studying root systems, pointed out that root studies are tedious and time consuming. The importance of belowground interference has been implied by some experiments. For example, Watt and Fraser (1933) demonstrated that removal of Scots pine (Pinus sylvestris) roots by trenching stimulated the root lengths of two understory species: wavy hairgrass (Deschampsia flexuosa) and wood sorrel (Oxalis acetosella).

Bohm et al. (1977), in a comparison of five methods for characterizing soybean rooting density, found that the trench profile method provided a good estimate of rooting density and was also fairly time efficient.

Effects of Herbivory on Individual Plants and Plant Community Structure

The population dynamics of a plant species are regulated by numerous ecosystem factors that could broadly be categorized as biotic and abiotic. The major biotic factors that act on a species are competition, herbivory, predation, and parasitism. Many ecologists believe that herbivory plays an important role in structuring present plant communities and in the evolution of their constituent species (McNaughton 1979, Crawley 1983). Herbivory may also influence plant distribution (Harper 1977). The impact of herbivory on the structure and species diversity of a plant community can be dramatic. For example, browsing by vertebrates on woody species can prevent successional change of grasslands into shrublands or woodlands. Conversely, prolonged heavy grazing by domestic livestock can convert semi-arid grasslands into barren scrub (Crawley 1983).

Selective feeding by herbivores may modify the competitive relationships among the component plant species of a community.

Diversity will usually increase when selective feeding on a previously dominant species reduces its vigor and allows the spread of less competitive, but more grazing tolerant plants (Harper 1969, Crawley 1983). On the other hand, selective feeding will usually decrease species diversity when a plant species that is uncompetitive in the absence of grazing achieves vigorous growth because competitively superior plants are eaten and it is avoided (Tansley and Adamson 1925, Chadwick 1960).

Livestock display a wide variety of feeding preferences. Sheep tend to select broadleaf herbaceous plants, while cattle prefer grasses (Cook 1983). Brush species are important in the diet of goats (Scifres 1981). Such variation in grazing habits and dietary requirements of different livestock species facilitate their use as agents of vegetation manipulation (Stoddart et al. 1975). Selective grazing is effective for weed control only when the right combination of plant species, class of animal, season of grazing, and stocking rate result in heavy grazing of undesirable plants to the advantage of desirable plants (Valentine 1979). Sheep may successfully be used to remove certain plant species not desirable for cattle. For instance, Johnson and Peake (1960) found that sheep grazing can reduce infestations of leafy spurge (Eurphobia esula). Scifres et al. (1971) reported suppression of common broomweed (Xanthocephalum dracunculoides) with sheep grazing. More recently, Sharrow and Mosher (1982) demonstrated control of tansy ragwort (Senecio jacobaea) with sheep grazing.

Insect herbivores for weed control have recently become increasingly popular, and in a number of cases successful. A classical case is the control of prickly pear cactus (Opuntia spp.) by the moth

Cactoblastis cactorum in Australia (Cussans 1974). Another example of effective biological control of a weed is that of St. John's Wort (Hypericum perforatum) in California using Chrysolina quadrigemmina (Huffaker and Kennet 1959). Recently, Maddox et al. (1986) have reported a great control potential of yellow star thistle (Centaurea solstitialis) by the seed-head weevil Bangasternus orientalis.

At the individual plant level, herbivory can, depending on severity, timing, and species, seriously impair the growth, vigor, and reproductive capacity of plants (Julander 1968, Heady 1975, Crawley 1983). Much range research effort has gone into investigation of impacts of intensity, frequency, and season of defoliation on the performance of individual plant species. Most of these investigations involved use of clipping techniques to simulate grazing. Despite various limitations, clipping studies can generate useful baseline information about critical periods of defoliation in plant species (Jameson 1963). Furthermore, Caldwell (1984) suggested that clipping studies possess direct management utility if three criteria are satisfied: (i) clippings are conducted with plants in a realistic environment, (ii) measured variables of plant performance are truly indicative of productive potential and competitive status in the community, and (iii) clipping methods approximate patterns and timing of defoliation of individual plants by grazing animals.

The impact of defoliation on plants is critically dependent on the severity and timing of attack relative to the plant's phenological stage (Heady 1975, Scifres 1981, Crawley 1983) and on the history of defoliation experienced by the plant (Crawley 1983). Trlica and Cook

(1971) found that salt desert plants defoliated late in the spring and at near maturity made little regrowth. Cook (1971) stated that defoliation was more injurious in the late spring or mid-summer than in the fall, winter or early spring for several desert species. Blaisdell and Pechanec (1949), studying arrowleaf balsamroot (*Balsamorhiza sagittata*), reported that total removal of herbage reduced the subsequent year's vegetative and flower stalk production. Clipping in May and early June (period of full bloom) was most harmful for this species. Complete defoliation was most detrimental for bluebunch wheatgrass (*Agropyron spicatum*) during the period of reduced regrowth before reproductive maturity (Blaisdell and Pechanec 1949). Stoddart (1946), studying the same species, also reported considerably less herbage yield when defoliation occurred later in the spring. Baker (1967), investigating two species each of grass, forb, and browse growth forms, showed that defoliation was most damaging during flowering and fruiting stages. Laycock and Conrad (1969) found that four years of successive clipping reduced herbage yield, stem height, and number of stems, and also delayed the development and flowering of tall bluebell (*Mertensia arizonica*). Clipping effects on tall bluebell were more severe at flowering and fruiting than at vegetative stages of growth (Laycock and Conrad 1969). Fuller (1985) found that aboveground clipping of dyers woad (*Isatis tinctoria*) during late June caused greater mortality and reduced flowering than clipping in early May.

Defoliation has also been shown to depress the reproductive capacity of plants. Stechman and Laude (1962), investigating four annual grasses common on California rangelands, demonstrated that height of the tallest head per plant, number of heads per plant, and mean seed weight all decreased with increased frequency and later timing of defoliation. Sackston (1959) reported that clipping sunflower (Helianthus annuus) reduced seed production and seed weight only at higher intensities (50% and 100% clipping by leaf area). The magnitude of response varied with the stage of growth at which plants were defoliated, being most severe at flowering (Sackston 1959). Other studies of defoliation effects have shown that reduction of seed production occurs over a single growing season (Jameson 1963, Maun and Cavers 1971, Reed and Stephenson 1972, Buwai and Trlica 1977, Lee and Bazzaz 1980).

Not much study has been devoted to root responses to grazing. Schuster (1964), working with Arizona fescue (Festuca arizonica), blue grama (Bouteloua gracilis), fringed sagebrush (Artemisia frigida), and rocky mountain pussytoes (Antennaria aprica), reported substantial impact on root patterns (root penetration, lateral spread) following three grazing treatments. Various other investigators have shown reduced root growth following defoliation (Biswell and Weaver 1933, Albertson et al. 1953, Crider 1955, Jameson 1963).

Despite an over-emphasis in the literature upon the negative impact of herbivory (Mattson and Addy 1975), it is becoming increasingly evident that positive aspects exist (Chew 1974, Harris 1974). McNaughton (1979), working in the Serengeti of East Africa, showed that plant productivity increased with level of herbivory. McNaughton (1979) found that protecting the grasslands of Serengeti for about 10 years reduced the relative proportion of the dominant grass Andropogon greenwayii from 56% to near zero. McNaughton's conclusion of grazing optimization has, however, been seriously questioned (Belsky 1986). More recently, Paige (1986) found that very high levels of mammalian herbivory on scarlet gilia *Ipomopsis aggregata* (95% removal of aboveground biomass) produced more flowering and subsequently higher seed output.

CHAPTER III

MATERIALS AND METHODS

Population Study

Study Site

A foothill site on the west slope of the Wellsville Mountains (Box Elder County, Utah, T12N, R2W, center of Section 32) between 1480 and 1525m elevation was selected to conduct population studies of dyers woad. The study site comprised a landscape broken into several narrow strips of rangeland running north-south, separated by wheat fields that were cultivated on alternate years. The slopes of the rangeland strips ranged between 6 and 20%. The soil was composed entirely of Sterling series, a loamy-skeletal, mixed, mesic Typic Calcixeroll, that was well drained. The study area was located on a mountain shallow loam range site in "good condition" for livestock (high seral ecological condition) (Soil Conservation Service 1967, 1975).

The major species of plants comprising the vegetation of these sites were [1]*Artemisia tridentata* Nutt, *Agropyron spicatum* (Pursh) Scrib. and Smith, *Bromus tectorum* L., *Poa secunda* Presl., *Allyssum alyssoides* L., *Balsamorhiza sagittata* (Pursh) Nutt., and other forbs. This study site had areas locally devoid of *Isatis tinctoria* L.

The estimated average precipitation on this site is 40cm per year (Soil Conservation Service 1975). Average annual air temperature is

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[1] Nomenclature of plants observed on study sites follow Welsh and Moore (1973).

9°C (Soil Conservation Service 1975). The study site has not been grazed by livestock for about 20 years.

Procedure

An area measuring 20 x 20m, and devoid of dyers woad was selected for this study. An area lacking in dyers woad was required to avoid problems of overlapping generations (Silvertown 1982) and age determination of biennials (Werner 1975b). The closest natural stand of dyers woad in any direction was 35m. Influx of dyers woad propagules into the study site was minimal. This was verified by analysis of soil seed reserves obtained in 80 randomly located soil cores. The soil cores were obtained by a soil auger measuring 6cm in diameter and driven to a depth of 15cm. Analysis of soil seed reserves was conducted during the last week of August 1984.

The 20 x 20m macroplot was gridded into twenty, 4 x 5m microplots permanently marked by stakes. Five of the 4 x 5m plots were randomly selected. These 4 x 5m microplots were further subdivided into twenty, 1 x 1m quadrats which served as sampling units. These units were also permanently marked at the four corners with steel concrete reinforcement rods. The 4 x 5m microplots had a 0.5m wide walkway in the middle to facilitate censusing. In total, there were one hundred 1 x 1m sampling units. On 8 September 1984, 1000 dyers woad seeds contained in their fruits were hand sown by surface broadcast on each 1 x 1m sampling unit. Seeds were collected in July 1984 from stands within 3km of the study site.

During fall 1984, dyers woad seedlings were marked within each sampling unit as soon as they could be positively identified.

Identification was usually possible at the four leaf stage. Seedlings were marked with colored toothpicks on a biweekly basis (Fig. 1). Toothpicks were removed as plants died, to allow determination of survivorship through time. The same process was repeated for seedlings that germinated during the spring of 1985. Similar procedures were used by Leverich and Levin (1979) and recommended by Werner (1975b). Separate sets of color-coded toothpicks were used for fall 1984 and spring 1985 populations (Fig. 1). Periodic censuses were conducted until the end of the experiment (Table 1).

Figure 1. Identification of established seedlings of dyers woad by color-coded toothpicks. For example, individuals germinating during spring 1985 were marked using red and blue combinations.

Table 1. Census dates for fall 1984 and spring 1985 populations of dyers woad.

Seasonal Conditions	Date Counts Made	Number of Weeks after Sowing
	22 Oct. 1984	6
	18 Nov. 1984	10
Snow cover and winter dormancy		
	8 April 1985	30
	15 April 1985*	31
	22 April 1985	32
	4 May 1985	34
	13 May 1985	36
	1 June 1985	38
	15 June 1985	40
Summer dormancy		
	16 Sept. 1985	53
	5 Oct. 1985	56
	19 Oct. 1985	58
Snow cover and winter dormancy		
	30 March 1986	81
	20 April 1986	84
	18 May 1986	88
	1 June 1986	90

*indicates date when censusing started for the spring 1985 population.

In addition to determining survivorship, rosette diameter and stalk height were measured periodically for each population by randomly selecting 30 plants within each category. On 19 June 1986, fruits were harvested from half of the surviving spring population. Fruit harvest was done for all individuals that germinated during the fall of 1984. The number of fruits per plant and fruit weights were then determined.

During the study, it was observed that germination and establishment of dyers woad was higher near sagebrush plants than in the interspaces between the shrubs. Because of inadequate sample size, it was not possible to do pairwise comparison of plants near sagebrush and in the interspaces for the fall 1984 population. A comparison of population responses to the two microsites was, however, possible for the cohort which began growing during the spring of 1985. The experimental procedure used to discern the effect of sagebrush microenvironment on the growth, development, and reproductive output of dyers woad was not robust. Consequently, the results can only serve to generate hypotheses about the influence of sagebrush microenvironments on population dynamics of dyers woad.

A 192hr Universal raingauge and a CR21 Micrologger (Campbell Scientific Inc., Logan, Utah) were set up on the study site in 1982 to collect data on precipitation and air temperature. Precipitation was monitored every 10 days during the snow free period and on a monthly basis during the winter. Due to technical problems, the temperature data were largely incomplete. To compensate for this problem and also obtain more long-term data, average precipitation and air temperatures were extrapolated from records obtained over the past 30 years at the

Corinne weather station. This station was located about 17km to the south of the study site at an elevation of 1410m.

Data Analysis

Survivorship data were analyzed as survivorship curves on a logarithmic scale to depict the stage(s) of growth at which plants were most susceptible to mortality. Due to uncontrolled variability under natural field conditions, an alpha of 0.1 was considered adequate for discerning biological differences. All statistical analyses for the population study were, therefore, conducted at $\alpha \leq 0.1$. Mean rosette diameter and mean stalk height of the fall 1984 and spring 1985 populations were distinguished using ninety percent confidence intervals. Within the spring population, a similar analysis was performed to test for differences between plants near sagebrush and in the interspaces. Mean fruit production of fall 1984, sagebrush associated (spring 1985 population), and interspace (spring 1985 population) individuals were separated using Duncan's multiple range test (Montgomery 1984). Ninety percent confidence intervals were constructed for the mean of each category. Fruit production was expressed on a per plant basis. A square root transformation was used to achieve equality of variances. A life-table analysis was performed for the combined populations by recognizing the following categories:

1. Seed bank.
2. Established seedlings (rosette diameter < 4cm).
3. Young rosettes
   - For fall population $<$ two growing periods.
   - For spring population $<$ one growing period.

For fall population $>$ two growing

4. Mature rosettes periods.
For spring population > one growing period.

5. Flowering individuals.

6. Mature individuals (produced seeds).

Transition probabilities were computed as the proportion of one category surviving to the next.

Seed Dispersal Study

Study Site

A foothill site on the west slope of the Wellsville Mountains (Box Elder County, Utah T12N, R2W, NE quarter of Section 32) between 1480m and 1525m elevation was selected as the study site. The native vegetation is broken into narrow strips of land running north-south between wheat fields that were usually cultivated on alternate years. The native areas were left uncultivated due to their steepness. The average slope of these west-facing slopes is between 15 and 20%. The chosen site was in "good" range condition (Soil Conservation Service 1975), having been ungrazed by livestock for about two decades. The dominant plants in this vegetation consisted of *Artemisia tridentata* Nutt., *Agropyron spicatum* (Pursh) Scribn. and Smith, *Bromus tectorum* L., *Isatis tinctoria* L., *Poa secunda* Presl., *Allyssum alyssoides* L., *Balsamorhiza sagittata* (Pursh) Nutt., and other short-lived forbs. The potential natural vegetation of the area is *Agropyron spicatum* dominated (Soil Conservation Service 1975).

The soil of the site was composed entirely of Sterling gravelly loam, a well-drained loamy-skeletal, mixed, mesic Typic Calcixeroll (Soil Conservation Service 1975). The estimated average annual precipitation and average annual air temperature were 40cm and 9°C, respectively (Soil Conservation Service 1975). An area measuring 120m by 1500m (18ha) on the eastern portion of the native strip was selected for conducting both the dispersal and clipping studies. The dispersal unit of dyers woad is the entire fruit. In the text, seeds and fruits are used interchangeably.

Procedure

An area measuring 30 x 40m was located within the study site. The area was selected on the basis of localized density of dyers woad. Efforts were made to work on isolated plants.

Nine fully mature plants with adequate seed production were randomly located within the "patchy" region of the macroplot. All attached fruits of these plants were sprayed with aerosol flourescent paints (DAZ-L green and orange paints). The paints served as markers so that detached fruits could be traced back to their respective sources. The selected plants were painted on 18 June 1985. Neighboring plants were sprayed with different colors in order to distinguish seeds of various plants. The minimum distance between neighboring plants was 3 meters.

The seed trap used was a modification of that described by Werner (1975a) and consisted of a 25 x 25cm masonite board. Four such boards were nailed on a wooden stake (approx. 1.5m long) leaving 6cm between each trap (Fig. 2). Four of these stakes were arranged around each plant so that they would radiate in each of the four cardinal directions (North, South, East, and West) at distances of 23, 54, 85, and 116cm from the plant. In total, there were sixteen (25 x 25cm) boards next to each plant. A central area beneath the plant (average radius = 10cm) was covered with a white flannel cloth to trap seeds that fell next to the mother plant (Fig. 2).

Figure 2. Layout of seed traps around a mother plant. Note that attached fruits are painted. Painting of fruits allowed them to be traced to their sources.

The masonite boards were smeared with Stikem® (Seabright Enterprises, California), a non-drying adhesive material mainly used to trap insects. This material, contrary to manufacturer specifications, had to be re-applied every 6 days to maintain its trapping capabilities. The number of seeds trapped on each 25 x 25cm board was counted and recorded on a daily basis at 5p.m. After the counts were completed, the seeds were removed from the boards to start a fresh count the next day. The dispersal study began on 25 June 1985 and data were gathered daily until 8 August 1985. Thereafter, plants were monitored less frequently until 27 August 1985.

A wind monitoring station, consisting of an anemometer and a wind vane, was set up at the study site on 23 June 1985 to record wind speed and direction. A datapod, Model 214 wind recorder (Omnidata International, Logan, Utah), was used as a sensor to read average wind speed, maximum wind speed, and their corresponding directions. The anemometer and wind vane were located one meter above the ground to reflect existing conditions at the height of the tallest dyers woad plants. Wind data collection was terminated after 20 days since there was little dissemination activity after this period.

Data Analysis

Seed density (number of seeds/fruits per unit area) was transformed into logarithmic (base 10) values and plotted against distance from mother plants, to test the fit of a negative exponential model. Several other equations were also fitted to the data. These included linear, quadratic, and power functions.

Root Study

Study Site

The root study was conducted in a sheep pasture 3km to the north of the dispersal, population, and clipping study sites. The pasture was also used for determining the degree of sheep utilization of dyers woad (Utilization Study). For description of the study site see page 35.

Procedure

Nine each of two categories of dyers woad plants were randomly selected in the middle section of the pasture in the last week of June 1985. The two categories were: rosette plants (average rosette diameter = 8.98cm) and mature individuals (produced seeds).

The root systems of these plants were studied using the trench profile method described by Bohm (1976, 1979). A trench, 50cm wide, 100cm long, and 150cm deep, was dug next to each plant using a backhoe on 14 July 1985. On average, the edge of the trench was 10cm away from the plant. The direction of each trench was randomly assigned to run either parallel or perpendicular to the slope, in order to determine any pronounced effect that slope may have on rooting pattern. The roots were exposed using small rakes, knives, screw-drivers, and garden trowels while working on the 10cm slice of soil towards the plants. A 100 x 100cm gridded frame was fixed to the profile wall to aid in mapping the root system. Exposed roots were mapped in their natural position, often simultaneously with the excavation, on a gridded paper at a scale of 1:5. About four hours were required to excavate and map each root system. In addition to the mapping which was done in situ, the root systems were photographed in their natural positions to provide any details overlooked while drawing the sketches in the field.

The root lengths were determined from drafted drawings of the field sketches using a Hipad digitizer (Houston Instrument, Austin, Texas). Total mapped root length and mapped taproot length within a 100cm soil profile were computed for each plant. The soil profile was divided into 5 sections, each 20cm deep. Total mapped root lengths were then determined for each soil section.

The soil of the study site was Sterling loamy-skeletal, mixed, mesic Typic Calcixeroll with a slope of 6 to 20 percent. Both runoff and the hazard of erosion were moderate. Available water-holding capacity before moisture depletion was estimated to be between 20 and 23cm (Soil Conservation Service 1975).

Data Analysis

The root data were analysed as a split plot design, with soil depth split on plant category. A two way analysis of variance was performed to test differences in root lengths, per m^3 soil layer, between plant categories and also between the various depths (Steel and Torrie 1980). The root data were also analyzed graphically by relating mapped root lengths to soil depth.

Clipping Study

Study Site

This study was conducted next to the dispersal study (see site description on page 26).

Procedure

A 30 x 50m macroplot with adequate populations of dyers woad in good condition native sagebrush-grass dominated vegetation was selected. The plot was divided into 30 rows, each 1m by 30m. The rows ran perpendicular to the slope and were separated by half meter walkways for ease of movement during data acquisition.

The clipping regime consisted of two intensities i.e., 60% clipping and 90% clipping plus a control. The percent aboveground phytomass removed was based on rosette radius, collective mid-rib lengths, and stalk height. The plants were subjected to varying frequency of clipping: (1) plants clipped only once (on 16 April 1986); (2) plants clipped twice (on 16 April and again on 7 May 1984); (3) plants clipped three times (on 16 April, 7 May, and 23 May 1984); and (4) plants clipped four times (on 16 April, 7 May, 23 May, and 11 June 1984) (Fig. 3). Each frequency-intensity treatment combination was replicated 30 times, so that in total 270 plants were used for this study. Plants were randomly selected within the entire matrix of the 30 x 50m macroplot.

At each clipping date, a separate set of previously unclipped plants, intermingled with the other multiple clipping set, was clipped at 90% intensity only once. This was to see if there was a time at which dyers woad was susceptible to a single, severe clipping. This treatment also yielded data to help in separating the interactions of frequency of clipping with time of clipping.

Data taken just before clipping (if applicable) for both sets of treatments included phenophase (Table 2), rosette diameter, number of rosette leaves, and basal diameter just beneath the rosette leaves. Other data collected at later dates were stalk height, number of stalks bearing flowers, and fruit number per plant.

Data Analysis

The statistical design consisted of a (2 x 4) + 1 modified factorial with experimental units (individual plants) arranged completely at random (a CRD). The treatments were assigned to the experimental units completely at random.

CLIPPING DATES

	16 APRIL	7 MAY	23 MAY	11 JUNE
FREQUENCY 1	X			
FREQUENCY 2	X	X		
FREQUENCY 3	X	X	X	
FREQUENCY 4	X	X	X	X

Figure 3. Number of times that dyers woad was clipped (frequency) and the corresponding dates of clipping during the spring of 1984.

Table 2. Phenological stages of Isatis tinctoria and corresponding numbers assigned to them. (Adapted from Fuller 1985).

Stages	Number
Dormancy	0
Leaf growth	1
Stem growth	2
Flowering	3
Seed development	4
Death	5

A binomial chi-square was used to test the effect of clipping on mortality and percent flowering of dyers woad (Cochran and Cox 1957). Ninety-five percent confidence intervals were used to detect differences between treatments in terms of seed production. A square root transformation was required to homogenize variances among treatments. For purposes of presentation, means and confidence intervals were back-transformed to the original scale (Sokal and Rohlf 1981). The multiple and single time clipping treatments were also analyzed together. Such analysis allowed determination of the proportion of the total effect accounted for by a single clip at a given time.

Utilization Study

Study Site

A foothill rangeland pasture on the west slope of Wellsville Mountains (Box Elder County, Utah T12N, R2W, SW quarter of Section 9), about 3km to the north of the population study site and at similar elevation, was selected for monitoring the utilization of dyers woad by sheep. This pasture was chosen because of a combination of private land-owner co-operation, tractable size, moderate terrain, moderate density of dyers woad, and because sheep had continually grazed there for the past decade.

The pasture was rectangularly shaped and entirely fenced except at the north end where the only watering source was located. The pasture measured approximately 450 X 1300m with a variety of topographic relief from steep hillside to flat ground and old roadbeds. The site was dominated by *Artemisia tridentata* Nutt., *Isatis tinctoria* L., *Bromus tectorum* L., *Poa bulbosa* L., *Gutierrezia sarothrae* (Pursh) Brit. and Rusby, and *Grindelia squarrosa* (Pursh) Dunal. The descriptions of range site associated with the Sterling soil series all indicate a potential natural vegetation comprised mostly of *Agropyron spicatum* (Pursh) Scibn. and Smith (Soil Conservation Service 1975). Thus, most of the pasture was in poor condition relative to both its ecological and livestock grazing potential (low seral).

The pasture was grazed by an unherded flock of about 150 sheep during the spring of 1984. The evidence of sheep usage was heaviest on the northern portion where sheep trails were most distinct. A piospheric study conducted on the pasture (West 1983a) indicated that there was a grazing gradient with utilization declining southwards on a north-south axis.

Procedure

A 30 x 50m macroplot was located near the center of the pasture. Utilization on dyers woad in this section was 75% (ocular estimate by grazed plant method, Stoddart et al. 1975) during spring 1983. Ten transects were randomly located and permanently marked using steel concrete reinforcement rods driven into the ground at 5m intervals. Only 20cm of the rods appeared aboveground in order to minimize effects on animal grazing behavior. The transects were chosen so that they ran parallel to the sheep trails which were generally oriented north-south. Six hundred plants (rosette diameter > 6cm) were randomly chosen using random distances along and away from the transects. The plants were further identified by colored toothpicks. Half of the selected plants were protected from grazing by $1m^3$ wire exclusion cages. These plants served as controls.

Beginning 27 April, 1984 the following observations were made biweekly (if applicable):

1. Whether the plant was grazed.
2. Remaining leaf length and widths on the grazed leaves (including petioles).
3. Rosette diameter.
4. Basal diameter.
5. Number of rosette leaves.
6. Number of flowering stalks.
7. Number of leaves on the flowering stalks.
8. Number of fruits per plant.
9. Fruit weight per 100 fruits.
10. Mortality on individuals.
11. Phenological stage of growth (Table 2).

With the exception of phenology, mortality, and reproductive variables (6 through 11), measurements on all other variables were discontinued after 20 May 1984 due to cessation of grazing on dyers woad by sheep.

A random set of 30 control plants were destructively sampled on 18 May 1984 to establish regression relationships between leaf area and leaf weight, and stalk height to stalk weight. The period between 27 April 1984 and 18 May 1984 represented maximum utilization on dyers woad.

Data Analysis

Regression analysis was used to evaluate the degree of sheep utilization on dyers woad. A chi-square test of independence was used to determine the effect of grazing on mortality and percent flowering of dyers woad (Steel and Torrie 1980).

CHAPTER IV

RESULTS AND DISCUSSION

Population Study

Field Establishment and Life Cycle

From 100,000 fruits collected during the summer of 1984 and sown on 8 September 1984, 285 individuals were established by October of 1984. Establishment was defined as the four-leaf stage when positive identification was possible. These plants overwintered as rosettes and remained vegetative during the spring of 1985. Plants that survived the subsequent summer drought numbered 36. These overwintered again as rosettes and all flowered and set seed in the spring of 1986 (Fig. 4).

During the spring of 1985, 2,664 plants established, none of which flowered the same year. During the spring of 1986, 87% of the 371 surviving individuals flowered and produced seeds, while 13% remained vegetative (Fig. 4). Further monitoring of field establishment showed that germination from the original seed input (8 September 1984) ceased after the fall of 1985.

These data demonstrate that, for freshly shed seeds, lower establishment rates (0.3%) occur in the fall than during the following spring (2.7%). On a northern Utah rangeland in good condition, dyers woad behaved predominantly as a biennial, with the potential to live longer than two years. The lack of germination after fall 1985 suggests that seeds of dyers woad may have limited endurance in the soil, undergo induced dormancy with time, or experience significant predation and/or pathogen attack. Some plants established outside the

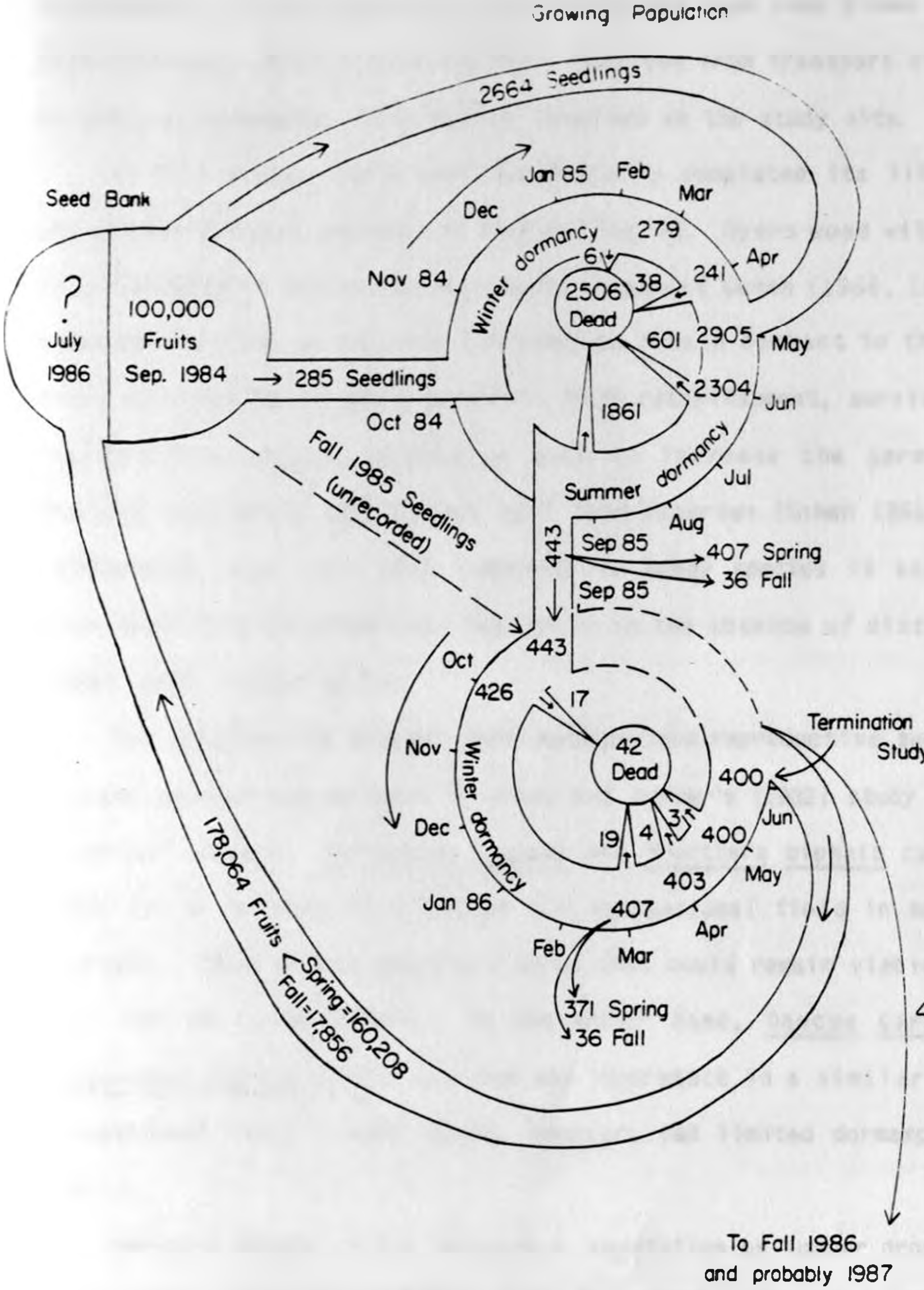


Figure 4. Population flux and life cycle of dyers woad on a good condition northern Utah rangeland (diagramatic model adapted from Sarukhan 1974).

experimental plots, suggesting that fruits may have been blown by wind. Alternatively, these plants may have resulted from transport of fruits by ants, a phenomenon occasionally observed on the study site.

In this study, dyers woad successfully completed its life cycle and produced large amounts of fruits (Fig. 4). Dyers woad will thus, in accordance with theoretical predictions of Cohen (1966, 1967), be expected to display minimal tendency to remain dormant in the soil. Under circumstances of relatively high establishment, survival, and reproductive output, selection acts to increase the germinating fraction and reduce the dormant soil seed reserves (Cohen 1966, 1967). Furthermore, high soil seed longevity in weedy species is associated with inability to complete life cycle in the absence of disturbance (Baker 1974, Harper 1977).

The relationship between seed dormancy and reproductive success of a plant species was evident in Gross and Werner's (1982) study of four "biennial" plants. Verbascum thapsus and Oenothera biennis could not establish or survive in a 15-year old successional field in southwest Michigan. These plants possessed seeds that could remain viable in the soil for 80 to 100 years. On the other hand, Daucus carota and Tragopogon dubius could survive and reproduce in a similarly aged successional field. Their seeds, however, had limited dormancy (< 2 years).

Periodic damage to the herbaceous vegetation by summer drought and cold winter conditions creates areas of sparse vegetation with sites suitable for recolonization at the beginning of fall and spring. Germination both in fall and spring allows dyers woad to take maximum advantage of these "windows of opportunity". Fall germinating individuals overwintered as rosettes and remained green despite some loss of turgidity. The retention of leaves means that plants are probably able to exploit mild periods within winter and carry out photosynthesis and possibly carry on belowground growth. These overwintering plants and spring germinating individuals probably embark on extraction of soil moisture and nutrients earlier than the established perennials, the growth of which comes much later. As argued by Harper (1977) timing of growth determines success of a species in a competitive situation, underscoring the significance of temporal control of germination. This notion is supported by the work of Sagar and Harper (1961) on mixtures of *Plantago* spp. and *Lolium perenne*. They showed that the relative success of these two species was easily and completely reversed by changing the relative time at which the components germinated and began growth.

Additionally, it can be said that by spreading germination over fall and spring seasons, dyers woad is buffered against environmental uncertainties and consequent severe reductions in populations. For example, an extremely harsh spring can probably be compensated for by populations from the fall season.

Germination during the spring of 1985 was an order of magnitude greater than during the fall of 1984 (Fig. 4). Casual observations indicated that germination rate during the fall of 1985 was similar to that of the spring of 1985. The lower germination rates during the fall of 1984 were not correlated with either precipitation amounts or mean monthly temperatures, since similarities occurred between fall 1984 and fall 1985 (Table 3). The seed source for the population study

Table 3. Precipitation (mm) and mean monthly temperatures (°C) recorded at or estimated for the study site during the autumns of 1984 and 1985.

	Year			
	1984		1985	
Month	Ppt.	Temp.*	Ppt.	Temp.*
August	17	21	0	20
September	65	15	57	14
October	32	7	40	8
November	65	3	87	0

*Extrapolated from Corinne Weather Station had some damaged fruits, although these were selected against during seed collection. Seed germination may have been easier from cracked fruits. The marked difference between fall 1984 and spring 1985 germination rates support findings of Young and Evans (1971), who demonstrated the existence of germination inhibiting substances in the fruits of dyers woad. Although tne full character and mode of operation of these substances are unknown, they have been determined to be autotoxic, water soluble, and therefore leachable (Young and Evans 1971). By remaining in the soil, the fruits could be exposed to varying degrees of soaking. By spring 1985, it is likely that enough leaching of the germination inhibitor would have occurred, enabling seeds to germinate in greater quantities. These germination inhibitors may contribute to the spread of germination over fall and spring seasons.

Plant Size and Reproductive Capacity for Fall and Spring Populations

Mean rosette diameter of fall germinating individuals was greater than that of spring germinating individuals on 23 May 1985 (Fig. 5). For both populations, rosette size increased during the remaining part of spring 1985 and were indistinguishable by 7 June 1985 (Fig 5). A substantial increase in rosette diameter occurred during the fall of 1985. The fall germinating population maintained nominally greater rosette sizes during most of the study period. The difference in rosette size between the two populations was most pronounced at the start of the spring 1986 growing season (30 March and 20 April; Fig. 5).

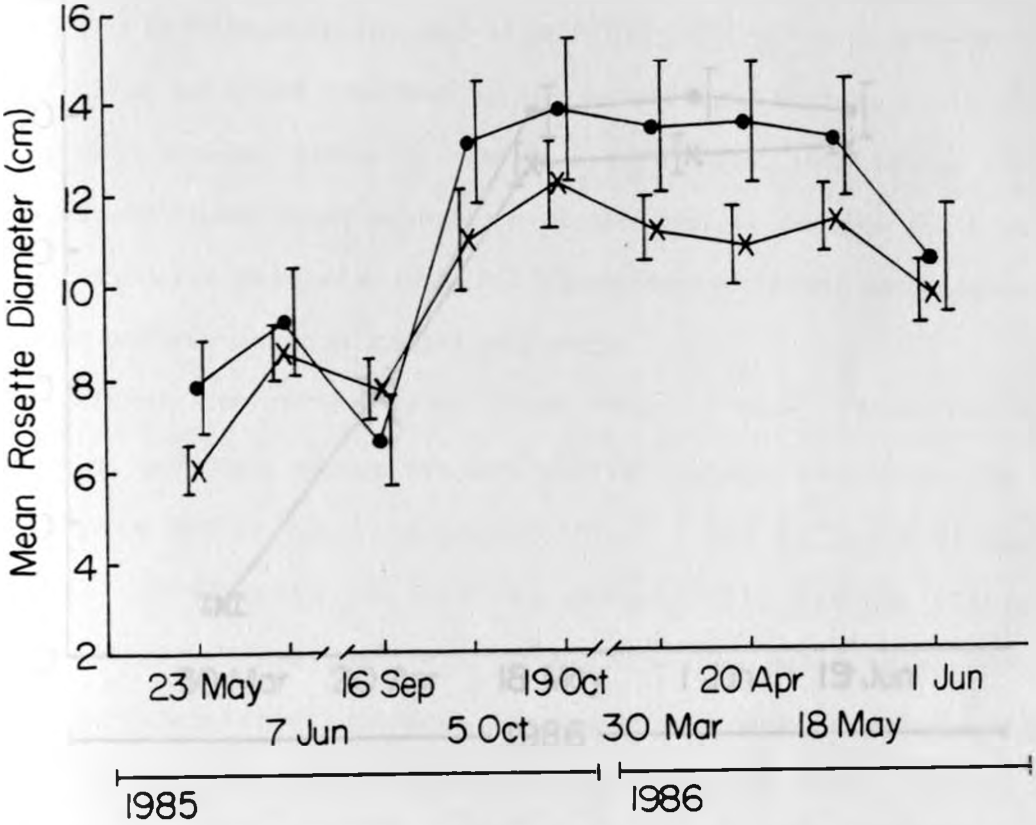


Figure 5. Mean rosette growth, 23 May 1985 to 1 June 1986, of dyers woad plants established during the fall of 1984 (●——●) and the spring of 1985 (×——×). Values are means of 30 plants. Vertical lines represent 90% confidence intervals.

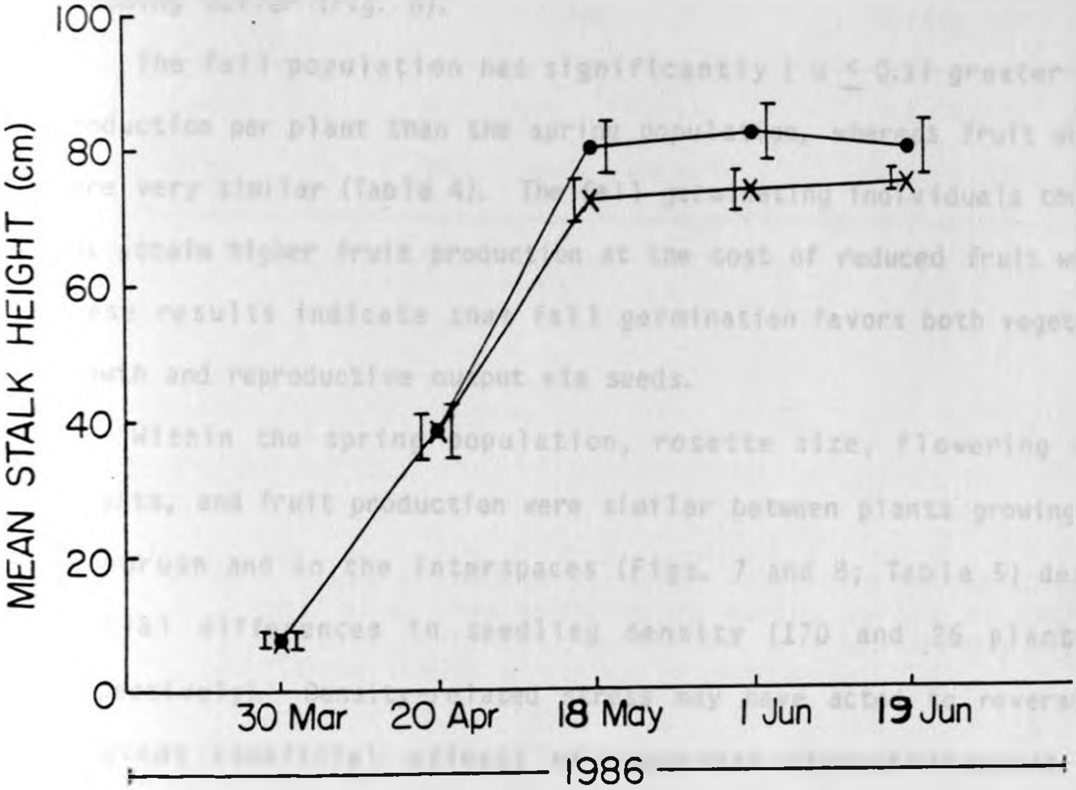


Figure 6. Mean height growth of flowering stalks, 30 March 1986 to 19 June 1986, of dyers woad plants established during the fall of 1984 (●——●) and the spring of 1985 (x——x). n = 30 plants. Vertical lines represent 90% confidence intervals.

In both populations, stem growth was initiated during the last week of March 1986. Rapid stem growth occurred up to 18 May 1986 during which time peak bloom was attained. Flowering stalk heights in the two populations diverged after 20 April with the fall population becoming taller (Fig. 6).

The fall population had significantly ($\alpha \leq 0.1$) greater fruit production per plant than the spring population, whereas fruit weights were very similar (Table 4). The fall germinating individuals thus did not attain higher fruit production at the cost of reduced fruit weight. These results indicate that fall germination favors both vegetative growth and reproductive output via seeds.

Within the spring population, rosette size, flowering stalk heights, and fruit production were similar between plants growing near sagebrush and in the interspaces (Figs. 7 and 8; Table 5) despite initial differences in seedling density (170 and 26 plants/m^2, respectively). Density-related stress may have acted to reverse the apparent beneficial effects of sagebrush microenvironment e.g., elevated nitrogen status, better soil moisture relations, and improved soil structure (Robertson 1947, Kline 1973).

The greater rosette size of the fall individuals almost two years after germination may have come about as a consequence of compounding of size through time, a characteristic feature of exponentially growing systems (Cook 1980a). In this manner, a small temporal separation in growth due to differential germination dates leads to large differences in size even when growth rates are similar. Because of low fall germination and lower established densities, intraspecific competition was probably reduced. The fall germinating individuals start spring

Table 4. Mean fruit production per plant and fruit weight/100fruits (grams) of fall 1984 (n = 34) and spring 1985 (n = 60) populations of dyers woad. Ninety percent confidence limits are shown in parentheses.

	Fall 1984	Spring 1985
Fruit number	563 (426, 681)	345 (281, 416)
Fruit weight	.390 (.380, .400)	.392 (.362, .442)

Table 5. Mean fruit production per plant and fruit weight/100fruits (grams) of plants germinating during spring of 1985 and growing in different microsites. n = 30. Ninety percent confidence limits are shown in parentheses.

	Plants near sagebrush	Interspace plants
Fruit number	293 (234, 359)	317 (225, 409)
Fruit weight	.391 (.361, .421)	.393 (.363, .423)

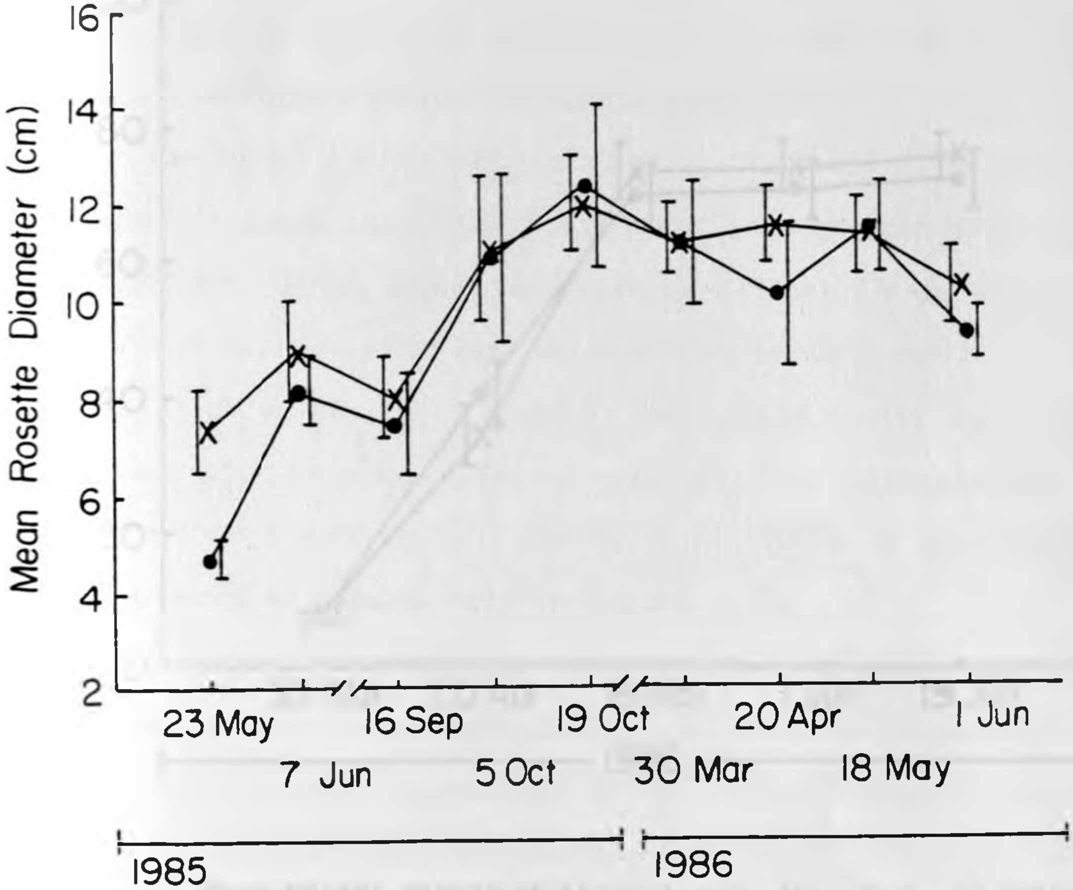


Figure 7. Mean rosette growth, 23 May 1985 to 1 June 1986, of dyers woad plants established near sagebrush (x——x) or in the interspaces (●——●). n = 30 plants. Vertical lines represent 90% confidence intervals.

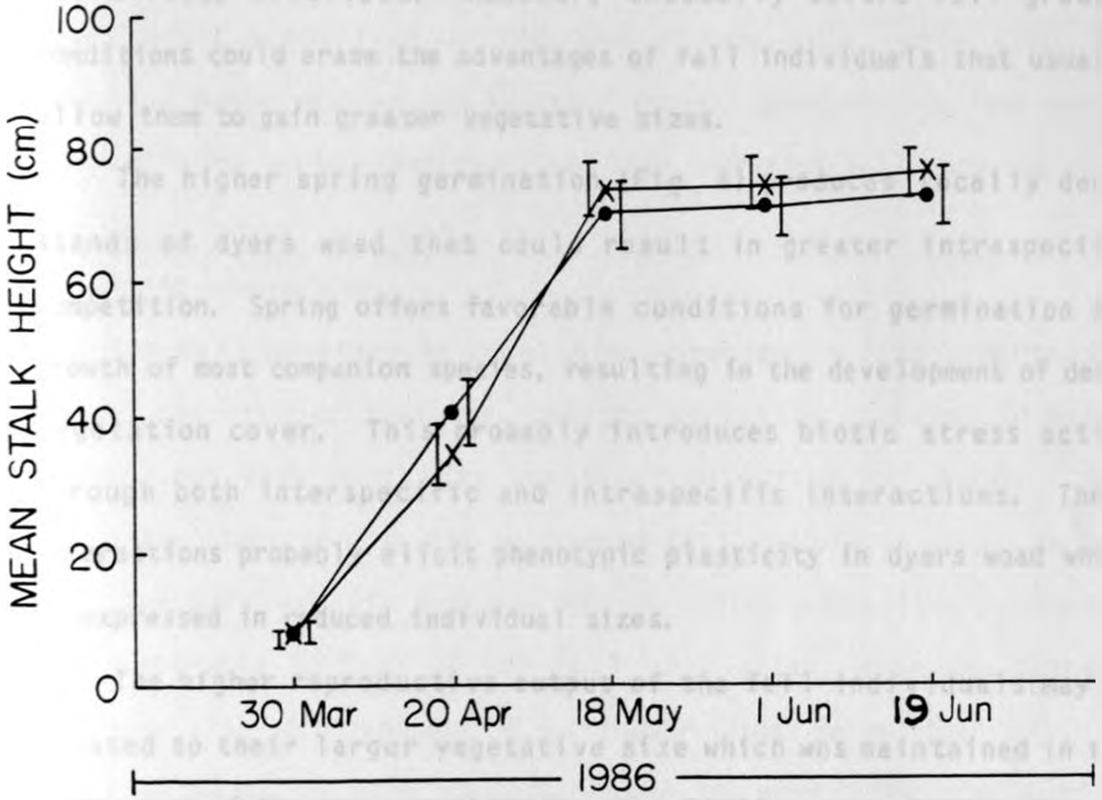


Figure 8. Mean height growth of flowering stalks, 30 March 1986 to 19 June 1986, of dyers woad plants established near sagebrush (x——x) or in the interspaces (●——●). n = 30 plants. Vertical lines represent 90% confidence intervals.

growth early, and thus may obtain a head start in extracting moisture and nutrient resources. Fall germinating individuals would also be expected to be superior in resource extraction since their root systems are already developed. However, unusually severe fall growing conditions could erase the advantages of fall individuals that usually allow them to gain greater vegetative sizes.

The higher spring germination (Fig. 4) produces locally dense stands of dyers woad that could result in greater intraspecific competition. Spring offers favorable conditions for germination and growth of most companion species, resulting in the development of dense vegetation cover. This probably introduces biotic stress acting through both interspecific and intraspecific interactions. These interactions probably elicit phenotypic plasticity in dyers woad which is expressed in reduced individual sizes.

The higher reproductive output of the fall individuals may be related to their larger vegetative size which was maintained in the major part of the study period (Fig. 5). Similar correlation between rosette size and fecundity was found for Senecio jacobaea (Van der Meijden and Van der Waals-Kooi 1979) and is reported to be widespread in short-lived perennials and biennials (Lacey 1986). Alternatively, if fecundity of dyers woad is density-dependent, and it is during the seedling stage when density effects are expressed, then fall germination would be expected to favor high reproductive output. Reduced fecundity under stressful environments (e.g. under dense vegetation) has been reported for several facultative biennials (Holt 1972, Werner 1975b, Harper 1977).

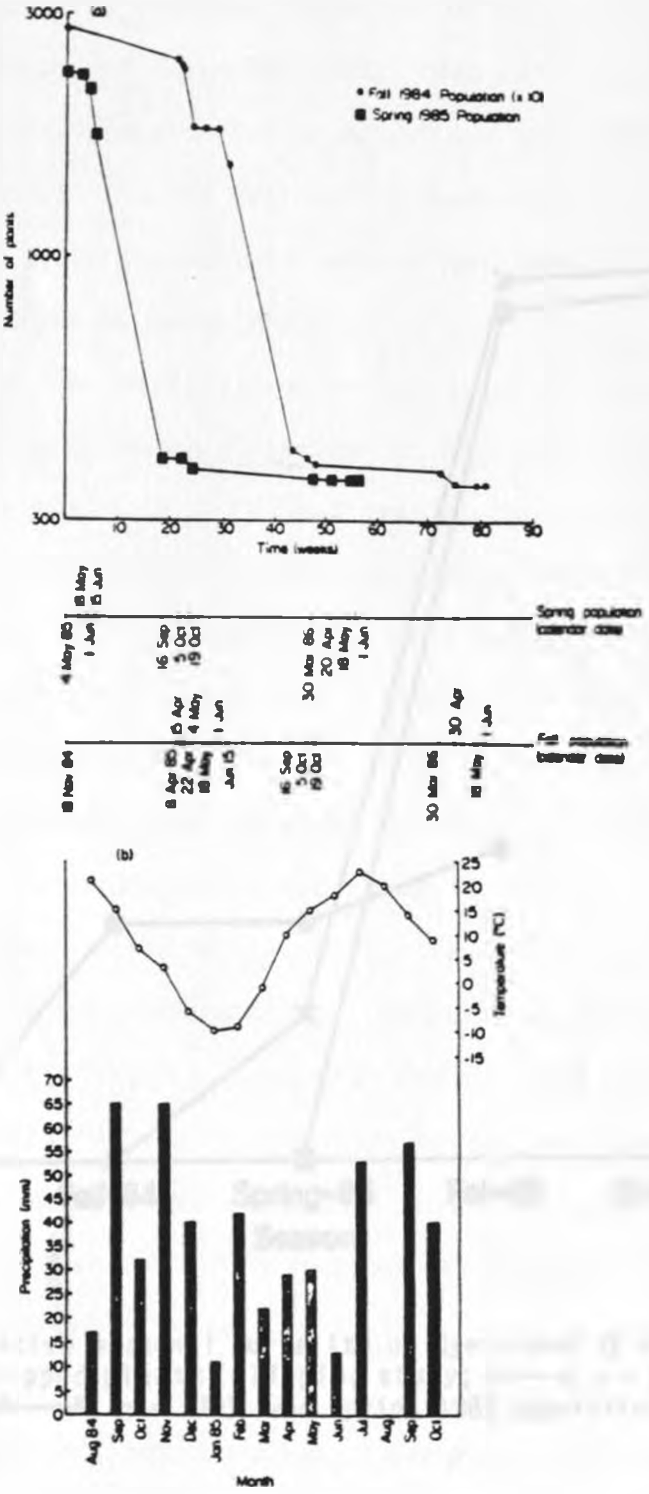
Despite higher fecundity per plant in the fall germinating individuals, in this study spring germination was more important in terms of overall population growth. Due to higher germination rates, the spring population was larger in size and thus contributed most to total fruit production at the end of the life cycle (Fig. 4). Selection may have operated to favor greater germinability and spread of germination across seasons rather than increased fall germination.

Survivorship Trend of Fall and Spring Populations

The fall germinating population experienced little mortality during the following winter. Slight mortality occurred in early spring, but peak mortality was observed during the summer. The population stabilized in the succeeding fall and winter (Figs. 9a and 10). The survivorship pattern for the spring germinating population was comparable to that of the fall population, with the highest mortality also occurring during the summer (Figs. 9a and 10).

A dramatic decline in population occurred for the spring population when plants were 10 weeks old. For the fall germinating population, this came after 30 weeks (Fig. 9a). At this time (15 June 1985), both populations had similar rosette sizes. The mean rosette diameter was 8.9cm for the spring population and 9.3cm for the fall population. Mortality trends of dyers woad may be more related to rosette size rather than age. This would conform to the notion that size is a better predictor of fates of facultative biennials than age (Werner 1975b, Werner and Caswell 1977, Van der Meijden and Van der Waals-Kooi 1979, Gross 1981).

Figure 9. Survivorship of dyers woad plants established during the fall of 1984 and the spring of 1985 (a) and monthly precipitation (mm) and estimated mean monthly temperatures (^{0}C) recorded for the study site betwen the fall of 1984 and the fall of 1985 (b). The horizontal lines between a and b indicate calendar dates at which plants were censused.


(a)
3000
1000
300
Number of plants
• Fall 1984 Population (x 10)
■ Spring 1985 Population
10
20
30
40
50
60
70
80
90
Time (weeks)
Spring population calendar date
4 May 85
18 May
1 Jun
15 Jun
16 Sep
5 Oct
19 Oct
30 Mar 86
20 Apr
18 May
1 Jun
Fall population calendar date
18 Nov 84
8 Apr 85
15 Apr
22 Apr
4 May
18 May
1 Jun
15 Jun
16 Sep
5 Oct
19 Oct
30 Mar 86
30 Apr
18 May
1 Jun
(b)
25
20
15
10
5
0
-5
-10
-15
Temperature (°C)
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Precipitation (mm)
Aug 84
Sep
Oct
Nov
Dec
Jan 85
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Month

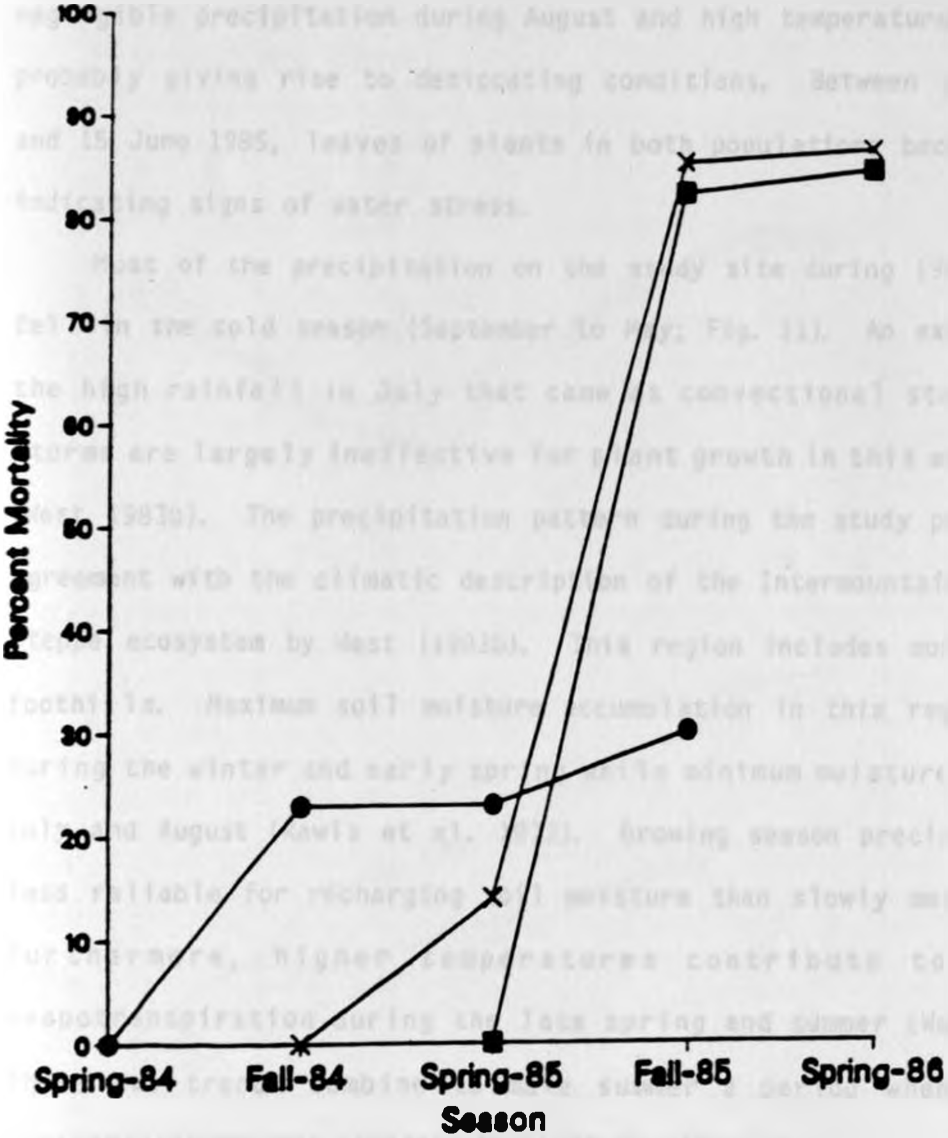


Figure 10. Cumulative seasonal mortality of dyers woad (% of initial numbers) for unclipped plants (clipping study; ●——●; n = 30), fall 1984 population (×——×; n = 279), and spring 1985 population (■——■; n = 2264).

The period of sharpest reduction in both populations was between 15 June 1985 and 16 September 1985. This period was characterized by negligible precipitation during August and high temperatures (Fig. 9b) probably giving rise to desiccating conditions. Between 1 June 1985 and 15 June 1985, leaves of plants in both populations became wilted, indicating signs of water stress.

Most of the precipitation on the study site during 1984 and 1985 fell in the cold season (September to May; Fig. 11). An exception was the high rainfall in July that came as convectional storms. Such storms are largely ineffective for plant growth in this environment (West 1983b). The precipitation pattern during the study period is in agreement with the climatic description of the Intermountain sagebrush steppe ecosystem by West (1983b). This region includes northern Utah foothills. Maximum soil moisture accumulation in this region occurs during the winter and early spring while minimum moisture occurs in July and August (Rawls et al. 1973). Growing season precipitation is less reliable for recharging soil moisture than slowly melting snow. Furthermore, higher temperatures contribute to greater evapotranspiration during the late spring and summer (West 1983b). These two trends combine to make summer a period when moisture availability becomes limiting to plant development.

As soil moisture recedes to deeper layers, it probably becomes out of reach of the developing roots of the young rosettes of dyers woad. Prevailing dry and hot conditions aboveground will tend to accentuate the degree of water stress experienced by the plants and thus make them susceptible to mortality. The shrivelled appearence of the rosettes in mid-June 1985 and virtual lack of herbivory and pathogen attack provide

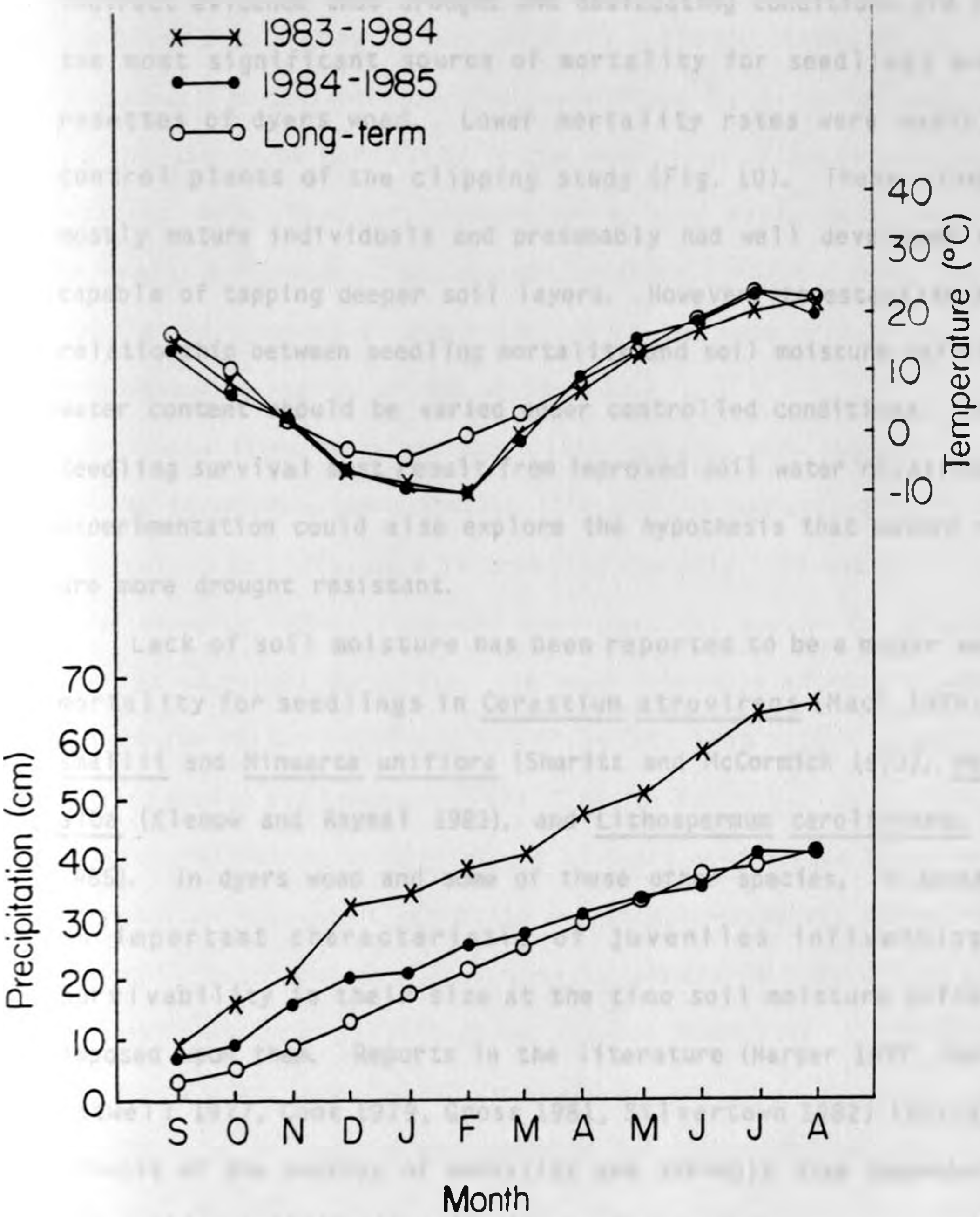


Figure 11. Accumulated precipitation (cm) and mean monthly temperatures during 1983-1984, 1984-1985, and their corresponding long term averages. Long term average precipitation and all temperature data were extrapolated from Corinne weather station. Corrine data covers a 30 year period.

indirect evidence that drought and desiccating conditions are probably the most significant source of mortality for seedlings and young rosettes of dyers woad. Lower mortality rates were exhibited by control plants of the clipping study (Fig. 10). These plants were mostly mature individuals and presumably had well developed taproots capable of tapping deeper soil layers. However, to establish a causal relationship between seedling mortality and soil moisture deficit, soil water content should be varied under controlled conditions. Increased seedling survival must result from improved soil water relations. Such experimentation could also explore the hypothesis that mature rosettes are more drought resistant.

Lack of soil moisture has been reported to be a major source of mortality for seedlings in Cerastium atrovirens (Mack 1976), Sedum smallii and Minuarta uniflora (Sharitz and McCormick 1973), Melilotus alba (Klemow and Raynal 1981), and Lithospermum caroliniense (Weller 1985). In dyers woad and some of these other species, it appears that an important characteristic of juveniles influencing their survivability is their size at the time soil moisture deficits are imposed upon them. Reports in the literature (Harper 1977, Werner and Caswell 1977, Cook 1979, Gross 1981, Silvertown 1982) indicate that effects of the sources of mortality are strongly size dependent, with the smaller individuals suffering greater hazards.

Mortality trends for dyers woad contrasts with those found in Plantago spp. (Hawthorne and Cavers 1976) and Ranunculus spp. (Sarukhan and Harper 1973) where death risks were relatively constant, though showing seasonal oscillation. For these herbaceous species, it was found that the greatest risk of death occurred during the period when survivors were growing most rapidly. Biotic stress resulting from intraspecific and interspecific competition for resources was suggested as the source of mortality in the seedlings of these species. Such studies were, however, conducted in more mesic environments. In contrast, the physical environment apparently plays a major role in the population dynamics of plant species in the more arid portions of the Intermountain region of the western U.S.

Mortalities for dyers woad plants growing near sagebrush and those in the interspaces were similar (73% and 74% respectively) in spite of a seven-fold difference in seedling density (170 and 26 plants/m^2). Thus density effect in dyers woad does not appear to be manifested through increased mortality. The more favorable microenvironment near sagebrush (Kline 1973) did not translate into better vegetative and reproductive performance (Figs. 7 and 8; Table 5). It is likely that density regulation in populations of dyers woad occurs by a combination of density-independent mortality and density-dependent fecundity. Such a proposition presumes that density stress is absorbed and expressed through phenotypic plasticity and reduced fecundity. Although a survey of dyers woad infestation in southeastern Idaho showed a negative correlation between plant density and height of flowering stalks (Callihan et al. 1984), the precise role of density in population regulation of dyers woad needs to be investigated via manipulative experimentation.

Plastic response to plant density has been demonstrated in some weedy species. A good example is Agrostemma githago (Harper 1960). When density of this species was increased, individual plants responded by branching more profusely and producing fewer seeds while mortality remained constant. As Harper (1960) pointed out, a weed that regulates its seed output as a function of population density possesses enormous resilience. In the case of A. githago, it was found that if populations were reduced by 90%, subsequent decreases in seed production were less than 10%. Density-dependent fecundity has important implications for control of weeds. For example, in dyers woad, reduction of populations would be more successful if undertaken during the early phase of spread, not when it has become a large scale infestation.

A life-table analysis for dyers woad showed constriction of population growth at two transitions; (i) seed to seedling (establishment) and (ii) young rosettes to mature rosettes. The combined establishment rate for the two populations was 3%. The transition probability for young rosettes was .23, i.e., only 23% of the young rosettes survived to mature rosettes (Fig. 12). Once plants became mature rosettes, the probability of surviving to a reproductive individual was .81. All flowering individuals set seed (Fig. 12). The life-table also reveals that the population of dyers woad, in terms of fruits, increased by 78% by the end of the life cycle. The weakest link in the chain of demographic events identified in this study was the young rosette (mortality = 77%).

Several studies have reported establishment and mortality patterns similar to that of dyers woad. Sagar (1970) noted that restriction of population size of Plantago lanceolata occurred at several stages of the life cycle, with major losses through failure to germinate and mortality of seedlings (> 65% died when less than 1 year old). Similarly, Foster (1964, In: Harper 1977), studying Bellis perennis and Palmbald (1968), working on Bromus inermis and Silene anglica, showed that constricted germination combined with seedling mortality contributed most to population regulation.

The life-table (Fig. 12) constructed for dyers woad has several limitations that make it inadequate to predict population growth. First, it does not account for the fate of most of the seeds originally sown (100,000 fruits). Soil seed pools are crucial components of the population biology of plant species (Harper 1977, Cook 1980b, Silvertown 1982) and hence should be considered in attempts to predict population changes over time.

Secondly, the life-table does not consider clonal growth. Dyers woad growing in other kinds of environments propagates vegetatively from crown buds (King 1966) and root buds (Gilkey 1957, J. O. Evans, pers. comm.). The life-table presented (Fig. 12) does not take account of demography of dyers woad at this level. Vegetative propagation did not occur in either population during the two year study period. Vegetative propagation occurs with greater likelihood in rosettes older than two growing periods (i.e. mature rosettes). Grazing or other mechanical damage stimulates vegetative propagation (Table 6; J. O. Evans, pers. comm.). The fates of mature rosettes (42 out of the 2543 established plants) were not followed in this study.

Observations of both mature rosettes and reproductive individuals from the clipping study showed that where plants were subjected to some damage (e.g., clipping), the chance of producing vegetative daughter rosettes, and subsequently flowering stalks was enhanced (Table 6). A

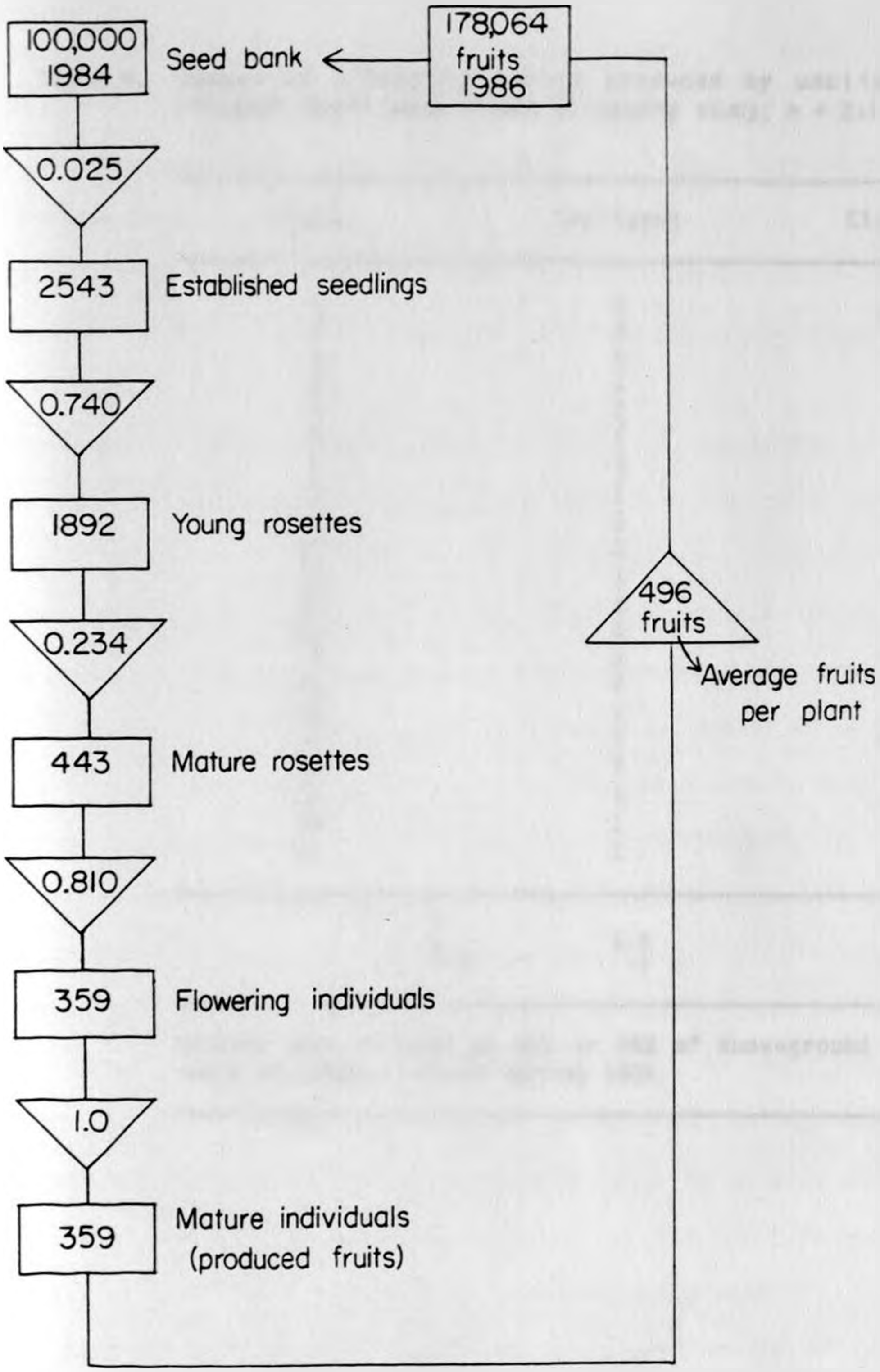


Figure 12. Life-table for a hand sown population of dyers woad established on a foothill rangeland site in eastern Box Elder County, Utah; 1984-1986.

Table 6. Number of flowering stalks produced by unclipped and clipped* dyers woad plants (clipping study; n = 21).

Plant	Unclipped	Clipped
1	3	3
2	2	2
3	1	2
4	1	2
5	2	3
6	1	2
7	3	2
8	1	3
9	1	2
10	2	2
11	1	2
12	1	3
13	1	2
14	1	2
15	2	2
16	1	2
17	1	1
18	1	4
19	1	1
20	1	1
21	1	1
$\bar{x}$	1.4	2.1
s.e	.1	.2

*plants were clipped at 60% or 90% of aboveground biomass, once or twice, within spring 1984.

similar response was reported for Senecio jacobaea following herbivore damage (Van der Meijden and Van der Waals-Kooi 1979). Vegetative propagules possess greater life expectancy than those derived from seed (Sarukhan 1974, Harper 1977, Grime 1979, Abrahamsom 1980). This alters the survivorship pattern of dyers woad in a manner which tends to ameliorate restriction of its population at the young rosette stage (Fig. 12).

Thirdly, the life-table analysis (Fig. 12) represents changes in two populations of dyers woad at one site and for only two years. During these two years (1984 and 1985), total precipitation was 18% above the estimated long term average, whereas effective precipitation i.e. that falling between September and May (West 1983b) was only 11% above normal. Mean monthly temperatures were slightly below the long term average (Fig. 11). Although the study period can be described as "typical", the data nevertheless lacks the variation inherent in year-to-year events. Recruitment, survivorship, and fecundity are likely to be governed by climatic variability (Jordan and Nobel 1979, 1981, Klemow and Raynal 1981, Mack and Pyke 1983, Reader 1985, Weller 1985) and habitat characteristics (Holt 1972, Hawthorne and Cavers 1976, Weller 1985). Therefore, this type of study should be replicated both in time and space to include the relevant range of abiotic conditions. Transition probabilities derived from such studies could form the basis for matrix modelling of population growth of dyers woad.

Establishment of the populations in an area devoid of dyers woad closely resembled an invasion into new territory. If conditions on the new habitat are suitable, it may be expected that high rates of population increase will be attained. This seemed to have been the case in this study because the population of fruits increased 78% by the second generation. It would be instructive to speculate on what might happen to this population some generations later. Density effects are likely to appear. These effects will probably be expressed through phenotypic plasticity and reduced fecundity. However, such mechanisms of population control may be mitigated by two forces: (i) chemical control of germination, and (ii) vegetative reproduction. Chemically controlled reductions of germinating seeds serves to limit population density of establishing plants, thus probably alleviating severe competition for resources. Individual plants will, in addition to sexual reproduction, be utilizing vegetative reproduction in order to multiply as the population grows and develops. This will be especially true under rangeland conditions where plants are exposed to higher risks of damage through herbivory and trampling effects. Vegetatively produced rosettes may combine low mortality risk with the capability to reproduce sexually.

Attempts to further quantify population changes in dyers woad will, therefore, require consideration of two things. First, the properties of germination inhibitors in dyers woad fruits will have to be discerned. Secondly, the relative contribution of vegetative and sexual reproduction to recruitment in a stabilized population will have to be ascertained.

The life-table (Fig. 12), even with its limitations, provides some insight into the life-history of dyers woad. Most mature rosettes had a high transition probability to the reproductive stage and produced large amounts of fruits ($\bar{x}$ = 496 per plant). Establishment was moderate and survival of juveniles (seedlings and young rosettes) in 1985 averaged 17%. This value is in excess of those achieved by many long-lived herbaceous perennials (Harper 1977, Weller 1985). Under more favorable spring conditions, juvenile survival for dyers woad was higher and estimated to be 35% (Fuller 1985). It thus appears, that on good condition (high seral) foothill rangelands in northern Utah, dyers woad would be favored to behave as a biennial with little benefit gained from long life-span (Harper and White 1974, Hart 1977, Cook 1979, Weller 1985). Results from the experimental population show that, dyers woad is capable of invading a well vegetated site that has not been grazed by livestock for several decades. This is contrary to the conventional wisdom that weedy species are locally 'doomed' in the absence of disturbance (Baker 1974, Harper 1977).

The invasive nature of dyers woad and its rapid spread in northern Utah may be due to more efficient utilization of environmental resources. Dyers woad germinates both in the fall and the spring, overwinters as a rosette, initiates early spring growth, has deep taproots (Table 10, page 82), possesses summer dormancy mechanisms (Fuller 1985), and has the ability to chemically inhibit germination and root elongation of some competing species (Young and Evans 1971). These characteristics probably allow dyers woad to escape from restrictions under which the native species are regulated.

Population Study: Implication for Biological Control

Seeds of dyers woad populations in North America have negligible dormancy (Young and Evans 1971, Evans and Gunnell 1982). Seed longevity beyond 10 months is unknown (Fuller 1985). In this study, seeds sown in September 1984 did not germinate beyond fall 1985. This observation and theoretical considerations would suggest limited seed endurance under natural conditions. Because field germination and establishment rates of dyers woad are on the order of 3%, its population growth would most likely be curbed by diminishing the ability to produce seeds. If seed production can be prevented for a few years, reduction in dyers woad populations is anticipated through exhaustion of soil seed reserves. To achieve this goal, however, a method of depleting existing vegetative individuals will have to be found.

Under conditions of continual disturbance, such as defoliation, flowering of dyers woad can be delayed (Fig. 27a and b, page 96). This is typical of many biennials and short-lived perennials (Harper 1977, Silvertown 1982). Dyers woad can switch to vegetative propagation through activation of buds located on the root crown and sometimes even the roots themselves (Gilkey 1957, King 1966, Varga and Evans 1978, Callihan et al. 1984). This mode of propagation is likely to be intensified by damage to individual plants. It is, therefore, difficult to decimate the vegetative portion of the population directly, especially when they are in the mature stages of growth. Mature rosettes have an 81% chance of survival and great potential for vegetative propagation.

Life-table analysis (Fig. 12) showed that the highest risk of mortality for dyers woad occurs at the young rosette stage. The natural mortality of individuals at this stage was 77%. Shoot damage will likely increase the risk of mortality of plants at this stage of development. Such a response may result from reduced development of the root system of the young rosette. Young rosettes, thus, become more susceptible to drought mortality. Dyers woad should be targeted for biological control at this vulnerable stage of development.

Seed Dispersal Study

The selected plants varied in stalk height, number of seeds at the start of sampling (Table 7), and percent seed fall at the end of the study (Table 8). Most of the seeds were shed in the first 10 days of the study; thereafter the rate of seed fall declined substantially, finally levelling off after 4 1/2 weeks (Fig. 13).

The seed dispersal pattern of dyers woad was fitted to several equations: linear, quadratic, two forms of exponential

$$(\log y = a + b_1 x + b_2 x^2 \text{ and } \log y = a + bx),$$

and a power function. Seed dispersal pattern of dyers woad was best described by a negative exponential model of the type $\log y = a + bx$; (Fig. 14). R-square values were used as the basis for selecting the best model.

Ninety-five percent of all the trapped seeds fell within 54cm of the mother plants. The greatest recorded distance that seeds moved from the source was 2.4m. The majority of the seeds were collected on seed traps located to the north and west of the plants (Fig. 15). This would indicate that wind influenced the landing location of seeds once they become detached from the plant. The relationship between wind speed and number of seeds scattered was poor on a day to day basis (Table 9). However, the effect of wind is likely to be expressed in a cumulative and indirect manner. This is supported by the fact that the

Table 7. Initial stalk height (cm) and number of fruits of dyers woad plants selected for the seed dispersal study.

Plant Number	Stalk Height (cm)	Number of fruits
1	71	2985
2	75	2160
3	69	2680
4	63	1863
5	60	1340
6	62	2110
7	59	1262
8	78	2396
9	82	3184
	$\bar{x}$ 69	$\bar{x}$ 2220
	s.e 3	s.e 210

Table 8. Percent fruit fall and the number of fruits remaining at the end of the seed dispersal study.

Plant Number	Percent fruit fall	Number of fruits remaining
1	89	328
2	95	115
3	80	540
4	94	149
5	94	82
6	80	418
7	83	210
8	89	258
9	96	128
	$\bar{x}$ 89	$\bar{x}$ 248
		s.e 49

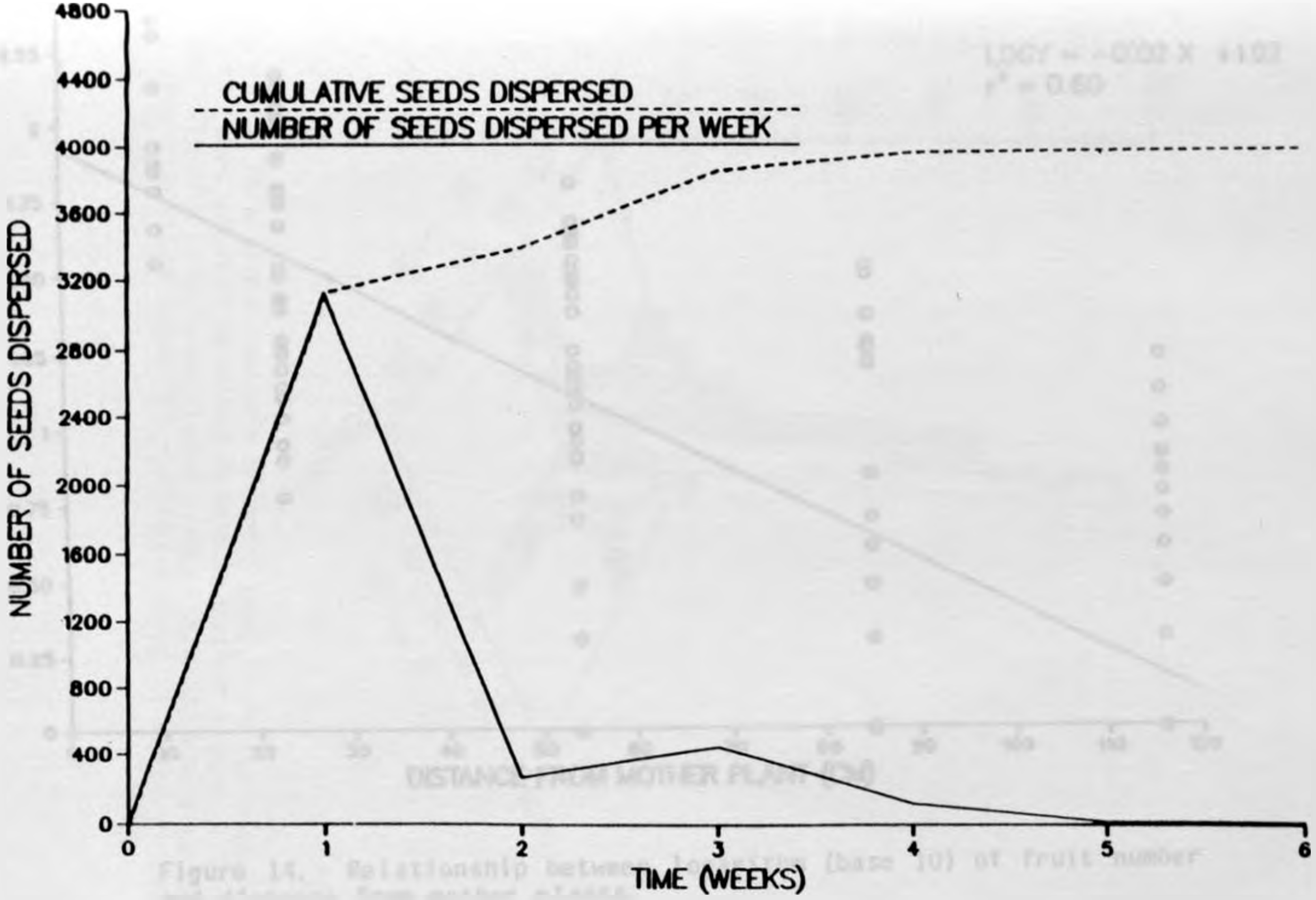


Figure 13. Dispersal of dyers woad seeds through time, showing number of seeds shed on a per week and cumulative basis, between 25 June 1985 and 8 August 1985.

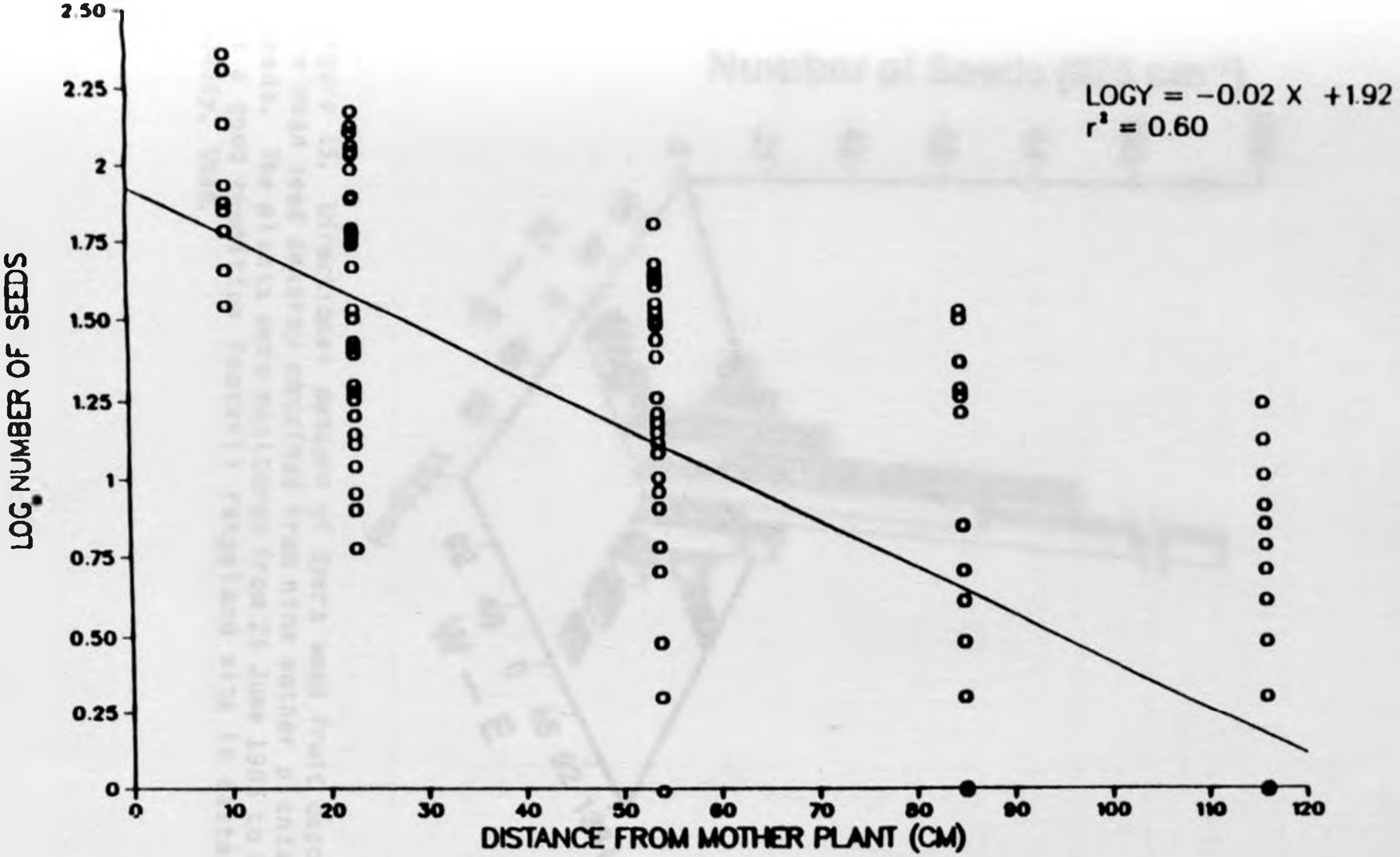


Figure 14. Relationship between logarithm (base 10) of fruit number and distance from mother plants.

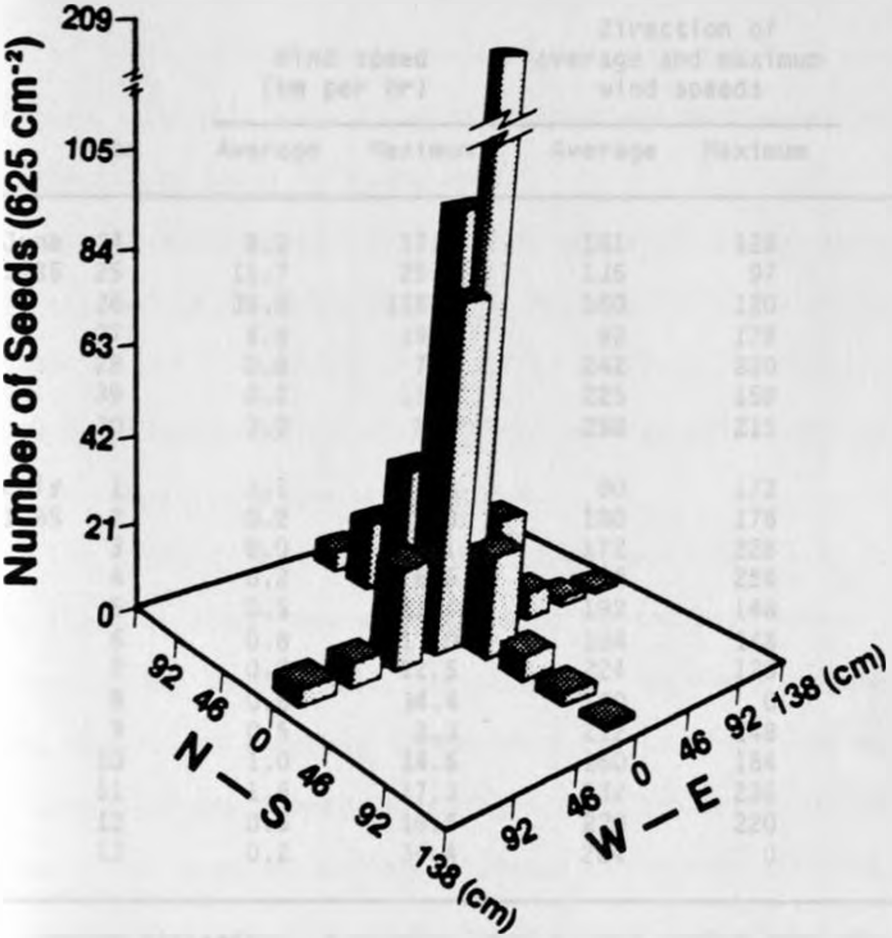


Figure 15. Directional pattern of dyers woad fruit deposition. Bars are mean seed density obtained from nine mother plants with marked seeds. The plants were monitored from 25 June 1985 to 8 August 1985 at a good condition foothill rangeland site in eastern Box Elder County, Utah.

Table 9. Wind speed (kph) and wind direction at the dispersal study site between 24 June 1985 and 13 July 1985 and corresponding number of fruits scattered.

		Wind speed (km per hr)		Direction of average and maximum wind speeds		Number of fruits scattered
	Date	Average	Maximum	Average	Maximum	
June	24	8.0	17.9	181	128	0
1985	25	11.7	25.6	135	97	164
	26	35.8	115.2	160	120	2449
	27	6.6	19.2	92	178	0
	28	0.8	7.7	242	210	190
	39	0.2	11.5	225	159	153
	30	3.0	8.6	258	215	74
July	1	1.1	5.8	90	172	98
1985	2	0.2	9.3	180	176	0
	3	0.0	2.1	172	228	77
	4	0.2	6.6	196	224	0
	5	0.5	11.4	192	148	0
	6	0.8	17.0	184	148	129
	7	0.2	12.5	224	128	62
	8	0.6	34.4	160	0	0
	9	0.5	8.3	212	248	0
	10	1.0	14.6	160	184	0
	11	1.6	17.3	232	236	103
	12	0.5	16.5	220	220	150
	13	0.2	34.4	204	0	122

*Wind direction: 0 or 360 means wind coming from the North
90 " " " " " East
180 " " " " " South
270 " " " " " West

prevailing wind direction was mainly toward the north and northwest over the 20 day recording period (Table 9). Also, since the fruits of dyers woad are firmly attached to the plants, some abrasive force such as wind and/or rain is required before they can be detached. Thus, the kind of tight relationship between rate of seed fall and wind speed observed in plants such as orchids (Howe and Smallwood 1982) would not be expected to apply to dyers woad.

The mean dispersal distance of seeds was positively correlated with the height at which they were released (Fig. 16). The tremendous growth of the flowering stalk after bolting, which implies a high resource allocation, may assist dyers woad to attain greater height and thus increase its dispersal distance.

The steep dispersal curve of dyers woad (Fig. 14) is similar to that found in other species where wind is the main agency of dispersal (Werner 1975a, Harper 1977, Cook 1980b). This study demonstrates that dyers woad is not commonly spread very far by wind. The rapid invasion and spread of dyers woad in northern Utah appears to be aided by other forces. For example, man may disperse the fruits of dyers woad on his shoes, truck tires or even in hay or straw bales that are carried to the mountains during hunting seasons. Livestock also could carry the fruits in mud on their hooves and help dispersal from spring to summer ranges.

The fruit pedicel of dyers woad functions like a hook and can stick to moving objects and thus facilitate animal dispersal. Some plants retain fruits past the first snowfall. The likelihood that herds of deer could encounter and disperse them increases during the

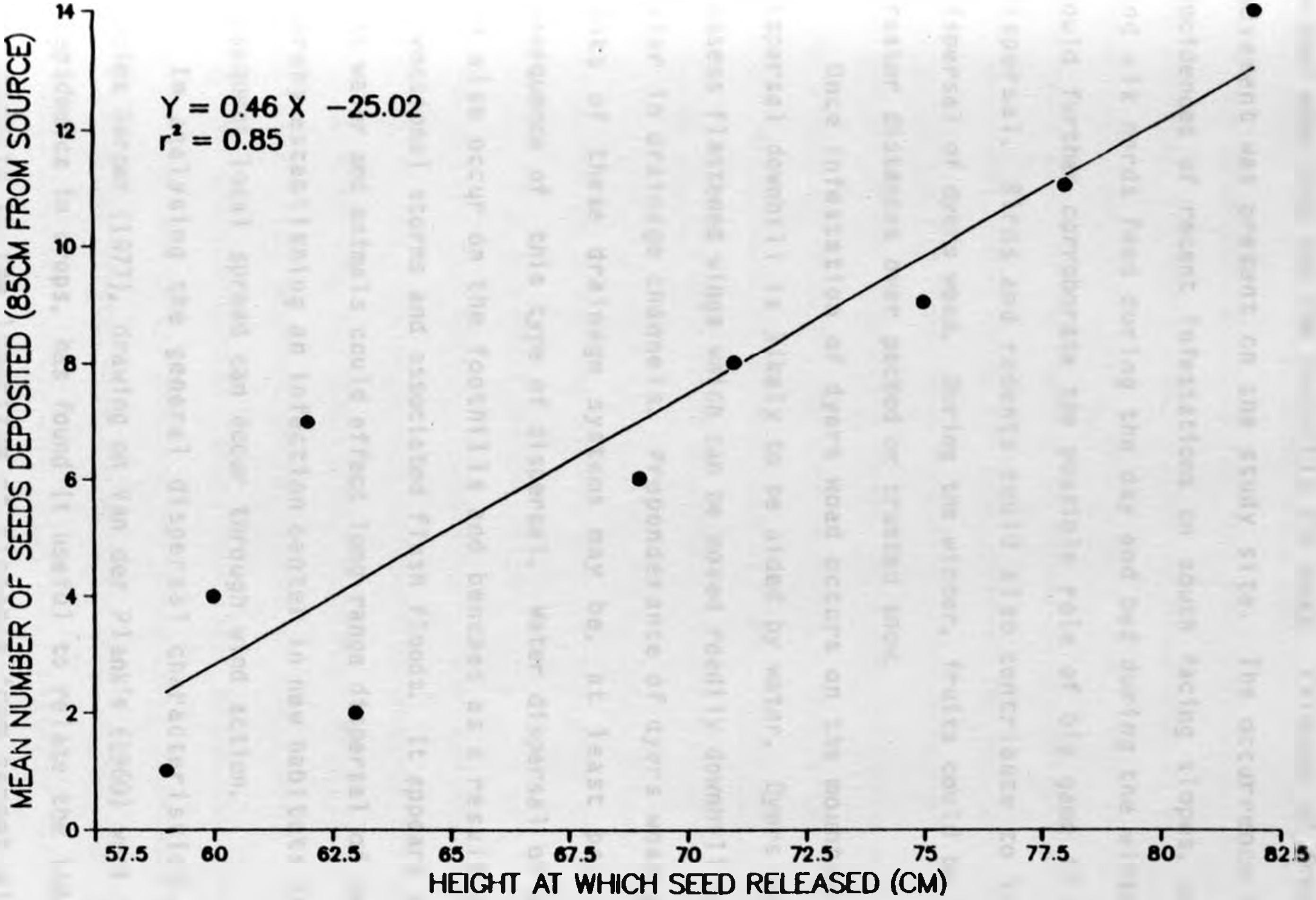


Figure 16. Relationship between mean dispersal distance and height at which fruits were released. Mean number of seeds per plant were 2,220.

winter when they use the foothills the most. Evidence of frequent deer movement was present on the study site. The occurrence of higher incidences of recent infestations on south facing slopes, where deer and elk herds feed during the day and bed during the winter nights would further corroborate the possible role of big game in effecting dispersal. Birds and rodents could also contribute to long range dispersal of dyers woad. During the winter, fruits could be blown for greater distances over packed or crusted snow.

Once infestation of dyers woad occurs on the mountain slopes, dispersal downhill is likely to be aided by water. Dyers woad fruits possess flattened wings which can be moved readily downhill by flowing water in drainage channels. Preponderance of dyers woad along the banks of these drainage systems may be, at least partially, a consequence of this type of dispersal. Water dispersal of dyers woad can also occur on the foothills and benches as a result of summer convectional storms and associated flash floods. It appears therefore, that water and animals could effect long range dispersal of dyers woad, thereby establishing an infection center in new habitats from which subsequent local spread can occur through wind action.

In analysing the general dispersal characteristics of plant species Harper (1977), drawing on Van der Plank's (1960) work on spread of epidemics in crops, has found it useful to relate the logarithm of seed density to the logarithm of distance from parent plant. He proposed that those species whose seed-dispersal curve has a slope equal to or steeper than an inverse square law will spread into colonizable areas as an advancing front. On the other hand, if the slope of the seed-dispersal curve is less than the inverse square law (less steep) it will lead to diffused patterns of isolated colonists which may subsequently act as foci for new infections. This procedure was performed for dyers woad. Figure 17 shows that it has a dispersal curve less steep than the inverse square line. This is an indication that dyers woad has the capacity to spread as an isolated colonist.

Watkinson (1978) using the same approach for the sand dune annual Vulpia fasciculata found that, depending on the height of inflorescence and percent ground vegetation cover, this species could spread either as an advancing front or isolated colonist. Similarly, species with special mechanisms of wind dispersal e.g., Senecio jacobaea and Tussilago farfara were found to possess dispersal curves less steep than the inverse square line. They were, therefore, considered to colonize not as advancing fronts but as isolated colonists over relatively large distances (Harper 1977).

The escape hypothesis of dispersal (Howe and Smallwood 1982) derives from the premise that disproportionate mortality exists near parent plants due to predation, pathogen attack or seedling competition. The seed-dispersal curve of dyers woad, like those species for which dispersal curves have been documented (Beattie and Lyson 1975, Werner 1975a, Marchand and Roach 1980), indicated that most of the seeds are dropped near the mother plant. Field populations of dyers woad display contagious dispersion patterns (Kirmse 1983), suggesting that adult distribution closely parallels seed distribution. No evidence of predation or pathogen attack was observed on experimental populations of dyers woad and mortality seemed to be density-independent.

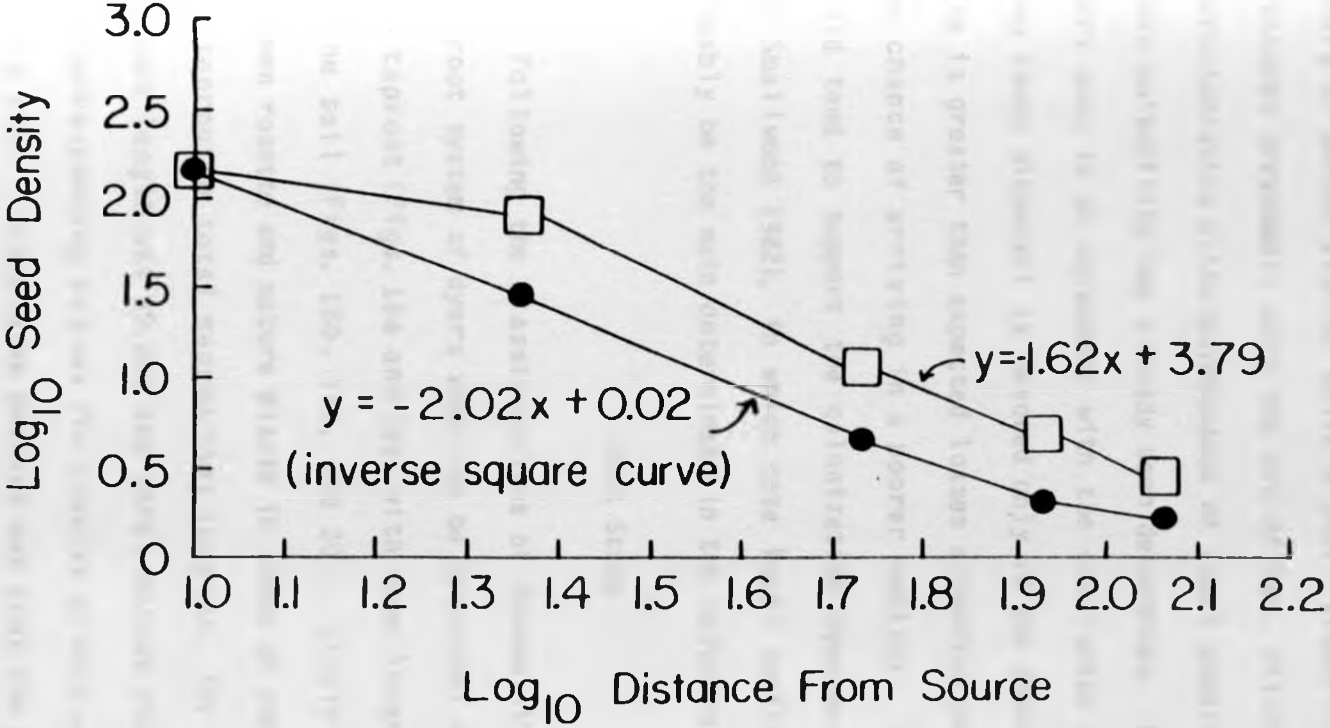


Figure 17. Seed density-source distance relationship (□——□) obtained from the dispersal study of dyers woad compared to the inverse square function (●——●).

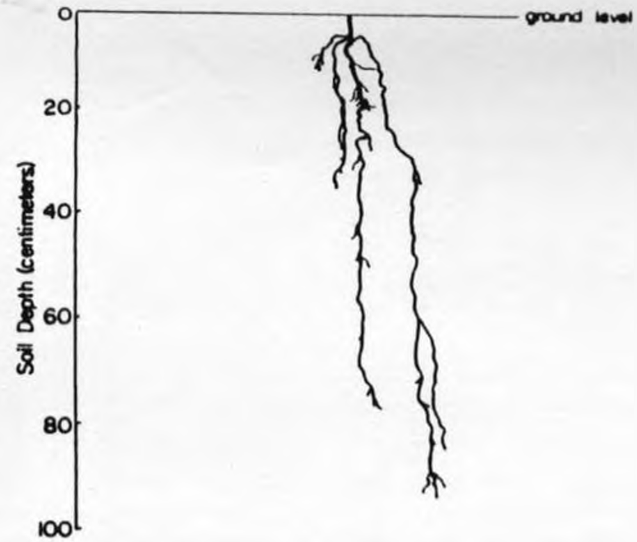
The dispersal method of dyers woad is likely to be one where the majority of propagules are deposited in a diffuse fashion within a few meters of parent plants, while a small proportion is carried for long distances presumably with the aid of man, wildlife, and water. These characteristics allow maintenance of local populations within a habitat whose suitability has already been determined. The dispersal scheme of dyers woad is in agreement with the conclusion of Gadgil (1971), that long range dispersal is favored only if the chance of reaching a better site is greater than expected losses attending the dispersal process or the chance of arriving in a poorer habitat. This dispersal method would tend to support the colonization hypothesis of dispersal (Howe and Smallwood 1982), in which case local spatial heterogeneity would probably be the main determinant in the colonization process.

Root Study

Following the classifications of Spence (1937) and Weaver (1958), the root system of dyers woad can be described as consisting primarily of a taproot (Figs. 18a and 19a) with some laterals in the upper 30cm of the soil (Figs. 18b, 19b, and 20). Little difference was found between rosette and mature plants in terms of the mean mapped length of the taproot or total mapped root lengths. For mature plants, mapped taproot length was 99.6cm and total mapped root length was 257.9cm. The corresponding values for rosette plants were 89.7cm and 216.9cm (Table 10). It should be pointed out that the trench profile method underestimates total root length since most of the fine roots are lost.

Figure 18. Selected photograph (a) and pictoralization of a representative root system (b) of dyers woad in the rosette stage of growth.

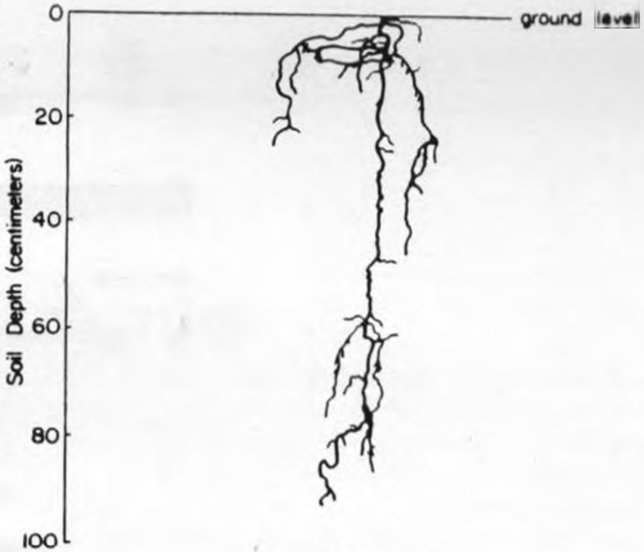
(a)



(b)

Figure 19. Selected photograph (a) and pictoralization of a representative root system (b) of dyers woad in the mature stage of growth.

(a)



(b)

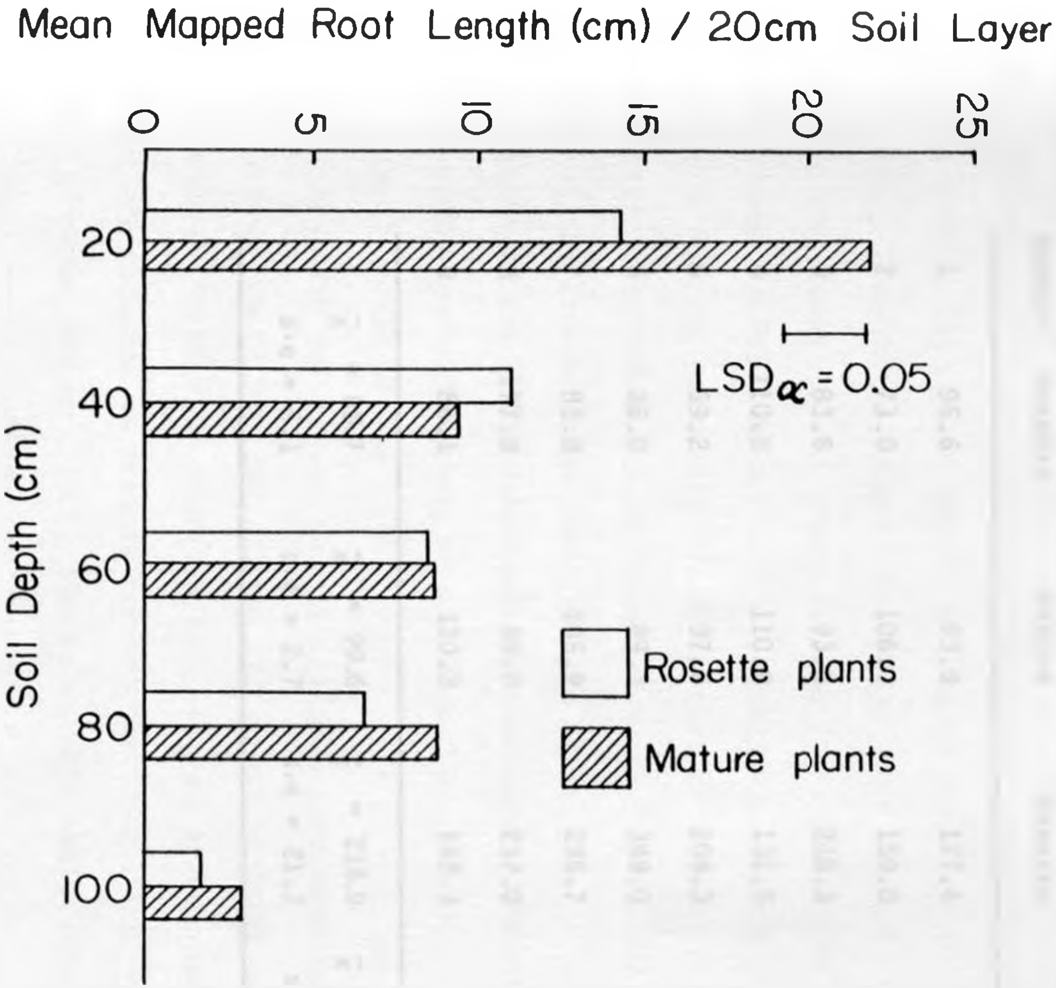


Figure 20. Histogram of mean mapped root length (cm)/20cm soil layer of mature and rosette plants of dyers woad in a soil profile. Values are means of nine plants in each age class.

Table 10. Mean mapped taproot and total mapped root lengths (cm) of rosette and mature dyers woad plants (mid-July 1985). Nine plants were used in each age class.

Plant	Taproot length (cm)		Total root length (cm)	
Number	Rosette	Mature	Rosette	Mature
1	96.6	93.9	177.4	247.9
2	73.0	106.0	159.0	455.9
3	83.8	93.8	218.3	278.6
4	110.8	110.8	132.5	169.7
5	69.2	97.6	204.3	264.7
6	86.0	89.3	349.0	148.7
7	83.8	105.9	285.7	278.4
8	177.8	89.0	257.0	198.8
9	86.1	110.3	169.3	278.1
	$\bar{x}$ = 89.7	$\bar{x}$ = 99.6	$\bar{x}$ = 216.9	$\bar{x}$ = 257.9
	s.e = 5.1	s.e = 2.7	s.e = 21.7	s.e = 28.1

Total mapped root lengths did not differ between the two categories, although there was a significant interaction effect between plant category and soil depth (Table 11). This indicates that rooting pattern in relation to soil depth differed between the two plant categories. The mature plants had greater root lengths in the upper 20cm of the soil, with 43% occurring in this soil layer. For the rosette plants, 31% of the mapped root length was found in this horizon (Fig. 20). Therefore, lateral branching near the soil surface may occur in the second year of growth because it is the mature individuals that showed the most marked lateral branching. Dyers woad seems to possess a rooting pattern similar to that of sagebrush, a pattern postulated to confer a strong competitive ability in the semi-desert steppe of the Intermountain West (Sturges 1977).

Davies et al. (1965) determined that moisture extraction profiles, and therefore depletion zones, of some annual crops closely paralleled the lateral spread of the roots. With a lateral root spread of about 40cm, dyers woad may create substantial water and nutrient depletion zones around itself that may depress the growth of neighboring plants. Furthermore, forbs with taproots and lateral spread near the soil surface are expected to present the greatest competition with grasses in dry climates (Weaver 1958). The relatively small total length of dyers woad roots compared to those of associated species e.g., bluebunch wheatgrass, does not necessarily mean that it has lower competitive ability. Smaller root systems do not exclude the possibility of higher root activity per unit length.

Although there appears to be a temporal separation between the aboveground growth of dyers woad and bluebunch wheatgrass (Agropyron

Table 11. Analysis of variance table for mapped root length (m/m^3 soil volume) variation with soil depth of two plant categories (mature and rosette individuals) of dyers woad in July 1985.

Source of Variation	df	SS	MS	Fcal
Plant category	1	2572.60	2752.60	1.41 ns
Error A	16	31228.16	1951.76	
Depth	4	77648.60	19412.15	34.14**
Category x Depth	4	10552.52	2638.13	4.64*
Error B	64	36385.87	568.53	

α = 0.05.
ns = not significant.
* = significant.
** = highly significant.

spicatum, a desirable native forage grass on northern Utah rangelands) during the spring and summer growing season, there was an overlap between the period of rapid growth of dyers woad (Fuller 1985) and that of peak water extraction of bluebunch wheatgrass (Thorgeirsson 1985) during the 1982 growing season. Whereas the calendar dates for these events are subject to yearly variability, it raises the possibility of belowground interference between these two species. More important, however, is the potential for dyers woad to suppress seedlings of more desirable forage species.

An important aspect of the rapid expansion of dyers woad may relate to its ability to initiate growth early in the spring, well in advance of associated perennial herbs. If this early growth proceeds concomitantly with root activity, then dyers woad may attain the advantage of resource acquisition in a relatively competition free environment. Thorgeirsson (1985), for example, demonstrated that the ability of crested wheatgrass (Agropyron desertorum) to extract water from deeper layers only two weeks earlier than bluebunch wheatgrass (A. spicatum) enhanced the ability of the former to compete against big sagebrush (Artemisia tridentata).

Clipping and Utilization Studies

On the site where the clipping study was conducted, unclipped dyers woad plants started vegetative growth by 16 April 1984, less than one week after snow melt. Stem growth was initiated during the last week of April while flowering began in the second week of May, reaching its peak about 23 May 1984. Seed formation occurred between 9 June and

15 June. By the end of June, most of the seeds had ripened (Fig. 21). In the grazed pasture, where sheep utilization of dyers woad was monitored, the phenological progression of the control plants was similar to those on the clipping study site (Fig. 22).

In the clipping study, the growth of control plants was also followed. Basal diameter increased during the period between 16 April and 7 May and thereafter remained fairly constant (Fig. 23). Likewise, rosette diameter increased during the period between 16 April and 7 May, levelling off by 23 May, after which it declined (Fig. 23). The decline in rosette diameter was due to withering of leaves which accompanied the growth and development of flowering stems. Stem growth started in the last week of April. Height of flowering stalks increased at a phenomenal rate during the period between 7 May and 11 June 1984 (Fig. 23). Thus, dyers woad was characterized by very rapid vegetative growth during spring that enabled it to produce seeds within two months after snow melt.

Effects of Multiple Clipping

Effects of multiple clipping on mortality, percent flowering, fruit production, and fruit weights of dyers woad were investigated. During the first year (1984), plants clipped at 60% intensity (low intensity) showed significant mortality over controls when clipped at least three times (Fig. 24a). For plants clipped at 90% intensity (high intensity), significant mortality over controls occurred in the first year when clipped at least two times (Fig. 24a). Over 1984 and 1985, at least three sequential clippings at either 60% intensity or 90% intensity carried out during the rapid growth season were required

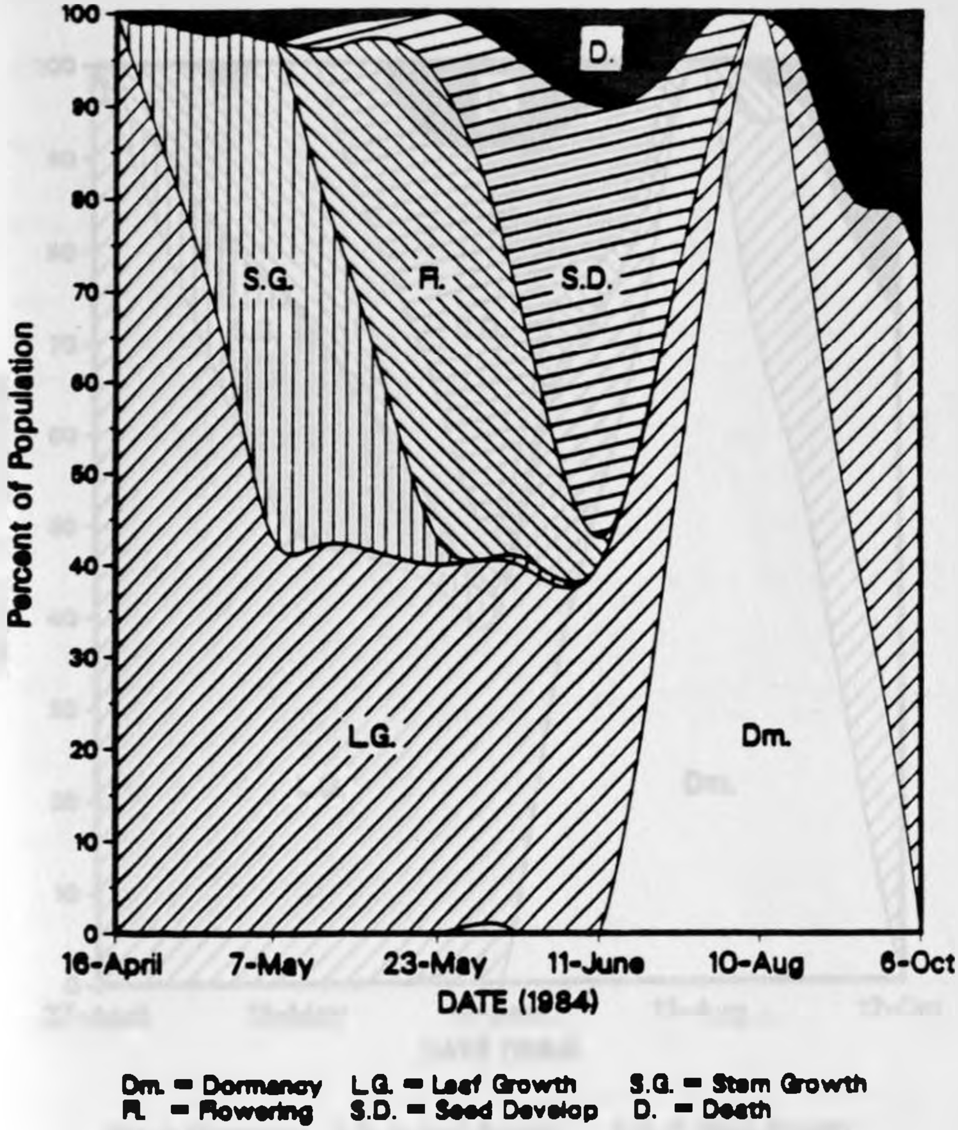


Figure 21. Percentages of unclipped dyers woad plants in various phenological stages during spring, summer, and fall of 1984 (clipping study). n = 30 plants.

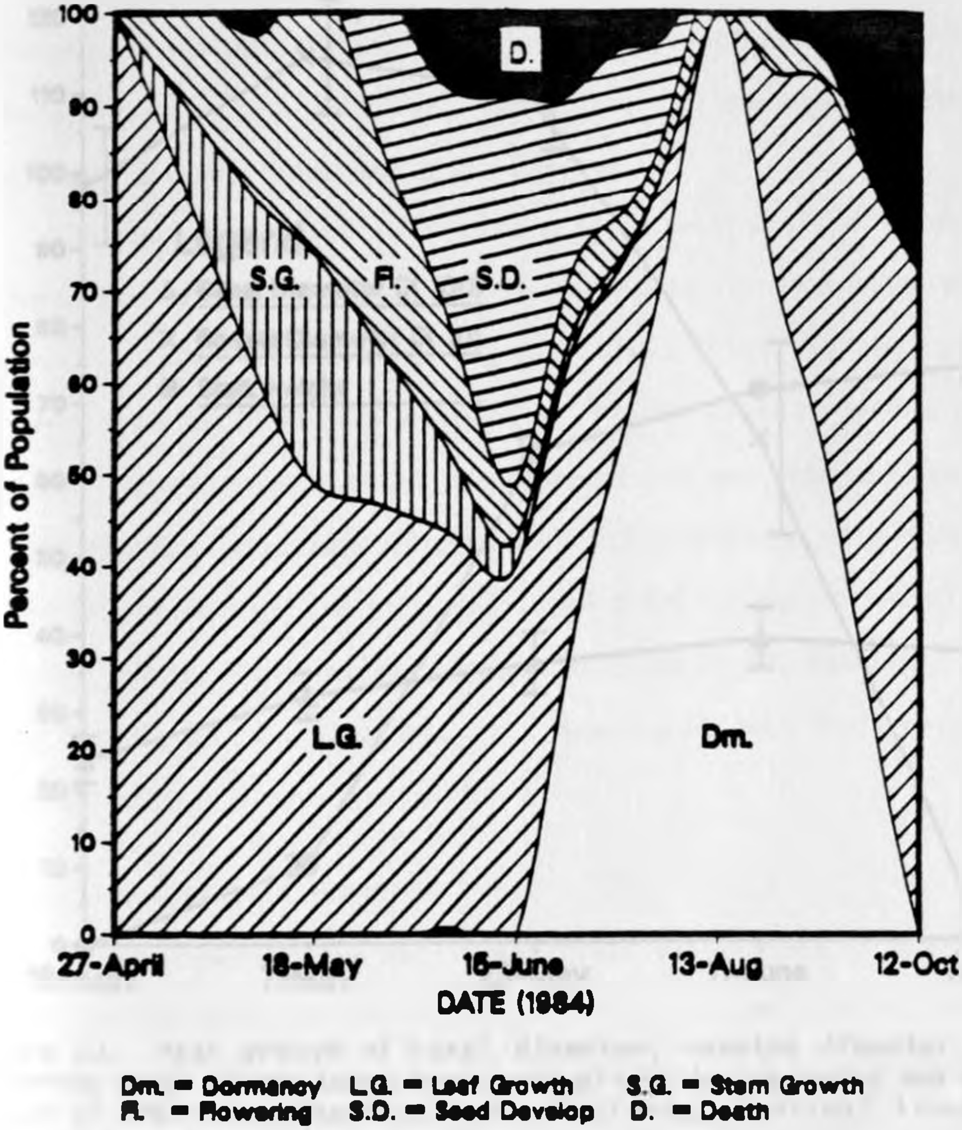


Figure 22. Percentages of ungrazed dyers woad plants in various phenological stages during spring, summer, and fall of 1984 (utilization study). n = 30 plants.

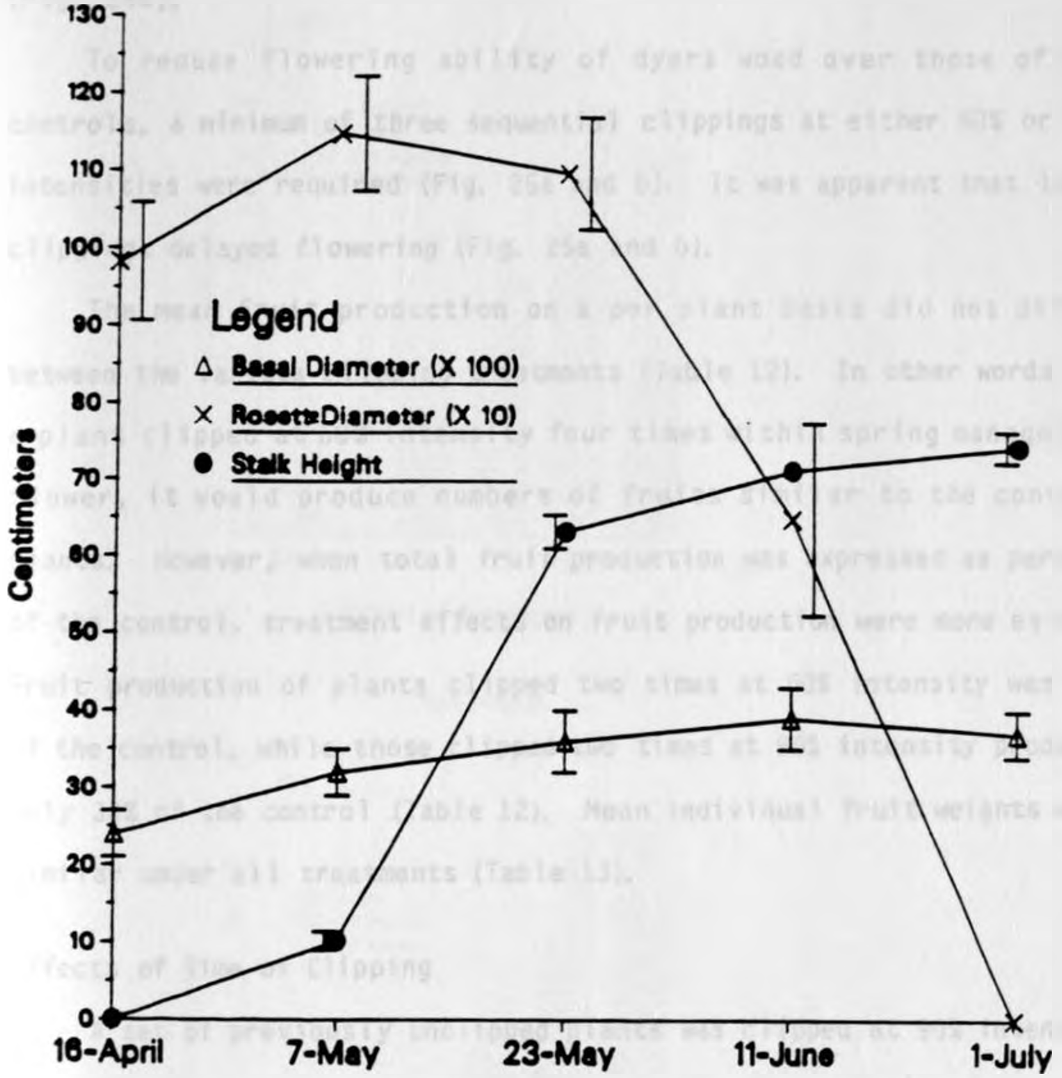


Figure 23. Mean growth of basal diameter, rosette diameter, and flowering stalk of unclipped dyers woad plants during spring and early summer of 1984 (clipping study). n = 30 plants. Vertical lines are 95% confidence intervals.

to significantly increase mortality rates over those of the controls (Fig. 24b).

To reduce flowering ability of dyers woad over those of the controls, a minimum of three sequential clippings at either 60% or 90% intensities were required (Fig. 25a and b). It was apparent that later clippings delayed flowering (Fig. 25a and b).

The mean fruit production on a per plant basis did not differ between the various clipping treatments (Table 12). In other words, if a plant clipped at 60% intensity four times within spring managed to flower, it would produce numbers of fruits similar to the control plants. However, when total fruit production was expressed as percent of the control, treatment effects on fruit production were more evident. Fruit production of plants clipped two times at 60% intensity was 49% of the control, while those clipped two times at 90% intensity produced only 38% of the control (Table 12). Mean individual fruit weights were similar under all treatments (Table 13).

Effects of Time of Clipping

A set of previously unclipped plants was clipped at 90% intensity only once in order to determine if there was a time at which dyers woad was susceptible to a single, severe clipping. This study showed that to achieve substantial mortality over those of the controls, plants had to be clipped at 90% intensity not earlier than 23 May (Fig. 26a and b). Single time clipping at 90% intensity prior to this period had no effect on the mortality of dyers woad (Fig. 26a and b). This clipping treatment resulted in substantial reduction in percent flowering only when plants were clipped on or after 23 May (Fig. 27a and b). A

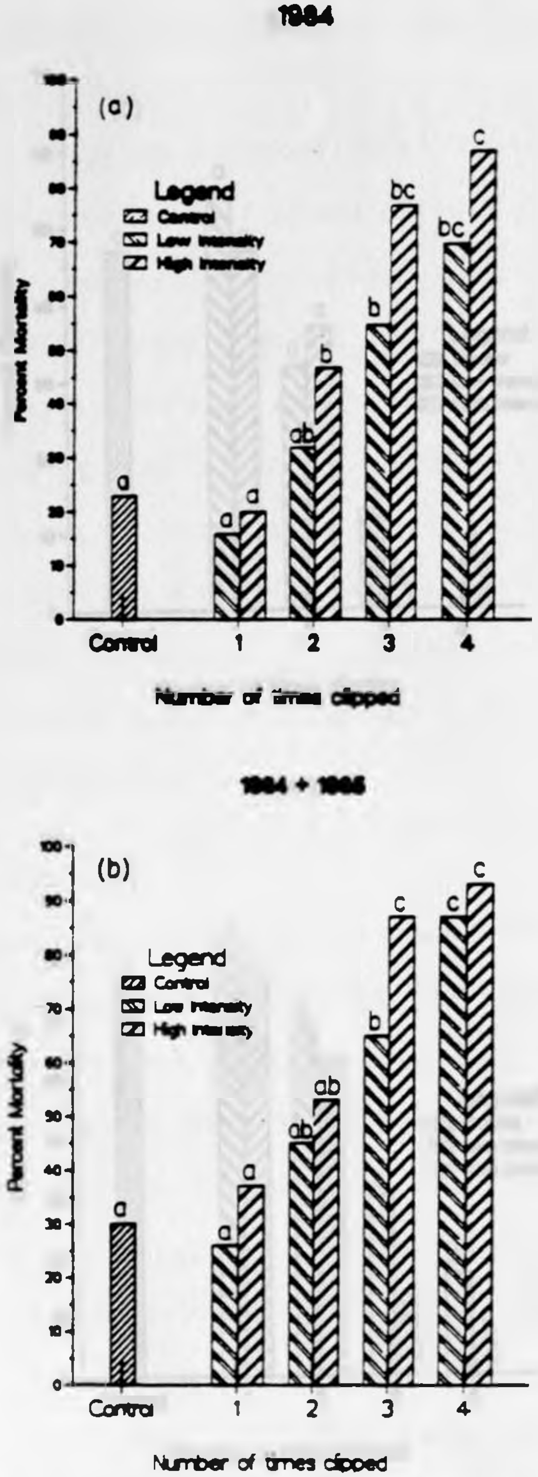


Figure 24. Effect of multiple clipping at two intensities (60% = low; 90% = high) on percent mortality of dyers woad during 1984 (a) and during 1984 and 1985 combined (b). n = 30 plants. Bars with different letters are significantly different at the 0.05 level.

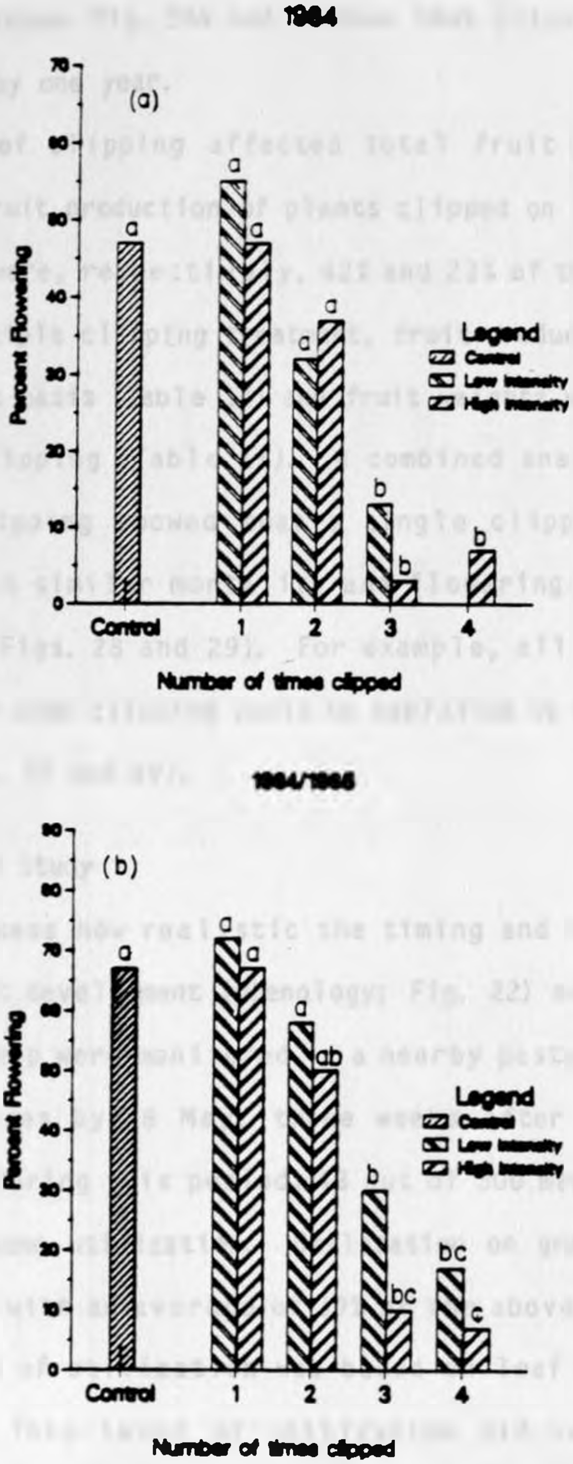


Figure 25. Effect of multiple clipping on percent flowering of dyers woad during 1984 (a) and during 1984 and 1985 combined (b). Intensities of clipping and sample size are the same as in Fig. 24. Bars with different letters are significantly different at the 0.05 level.

contrast between Fig. 26a and b shows that clipping after 7 May delayed flowering by one year.

Date of clipping affected total fruit production of treated plants. Fruit production of plants clipped on 7 May and those clipped on 23 May were, respectively, 42% and 23% of that in the control. As in the multiple clipping treatment, fruit production did not decline on a per plant basis (Table 14) and fruit weights were not affected by the time of clipping (Table 15). A combined analysis of multiple and single clipping showed that a single clipping at 90% intensity, resulted in similar mortality and flowering responses as multiple clipping (Figs. 28 and 29). For example, all the effect associated with a four time clipping could be explained by a one time clip in mid-June (Figs. 28 and 29).

Utilization Study

To assess how realistic the timing and intensity of clippings were, plant development (phenology; Fig. 22) and utilization of dyers woad by sheep were monitored in a nearby pasture. Sheep switched to other forages by 18 May, three weeks after grazing began on the pasture. During this period, 48 out of 300 marked dyers woad plants (16%) had some utilization. Utilization on grazed plants ranged from 18% to 92% with an average of 39% of the aboveground tissue removed. The degree of utilization was based on leaf area and stalk weight removed. This level of utilization did not have any effect on mortality, percent flowering, and mean fruit production (Table 16). As had occurred in the clipping treatment, fruit weights were not affected by grazing (Table 16). The basal diameter and rosette diameter of

Table 12. Fruit production of dyers woad plants clipped at varying intensities and frequencies during the spring of 1984.

Treatment*	Original Sample Size	Number that Fruited	Mean Fruit Production	95% Confidence Limits	Total Fruit Produced	% of Control
0 0	30	20	237	175, 318	4740	100
1 1	31	22	223	167, 286	4906	104
1 2	31	18	128	83, 184	2304	49
1 3	31	9	97	40, 179	873	18
1 4	30	5	139	39, 301	695	15
2 1	30	20	174	123, 234	3480	73
2 2	30	15	121	72, 181	1815	38
2 3	30	3	94	2, 436	282	6
2 4	30	1	164	----	162	3

*First digit refers to intensity of clipping (0 = control; 1 = 60%; 2 = 90%), while the second digit indicates number of times a plant was clipped.

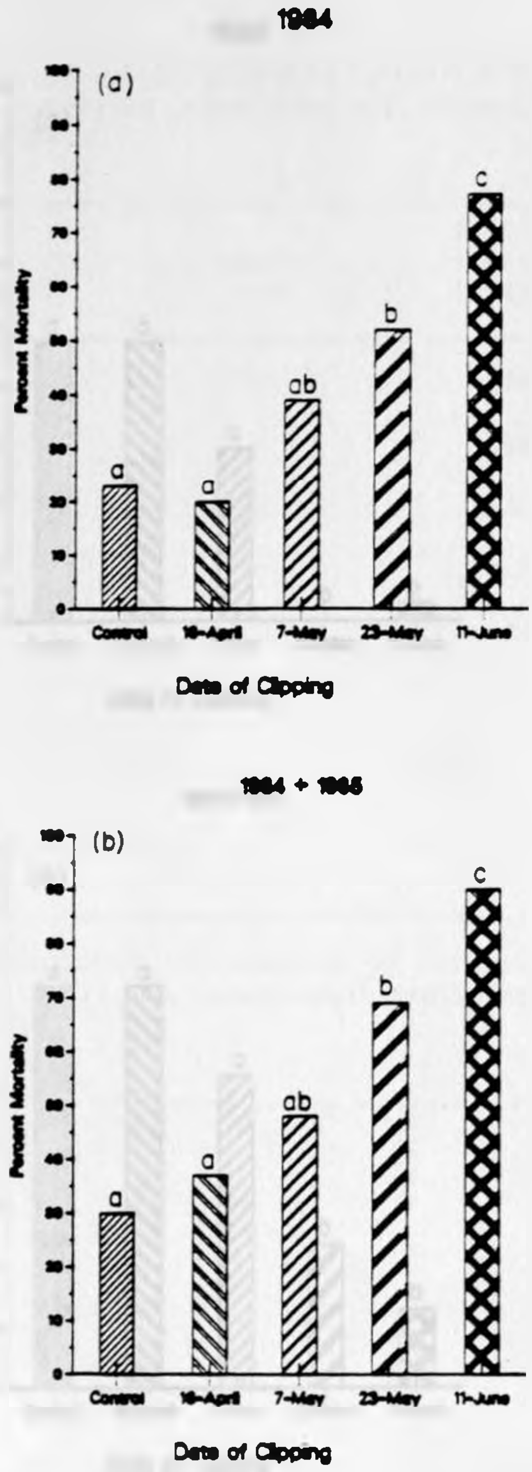


Figure 26. Effect of time of clipping on percent mortality of dyers woad during 1984 (a) and during 1984 and 1985 combined (b). Plants were clipped at 90% of aboveground phytomass. n = 30 plants. Bars with different letters are significantly different at the 0.05 level.

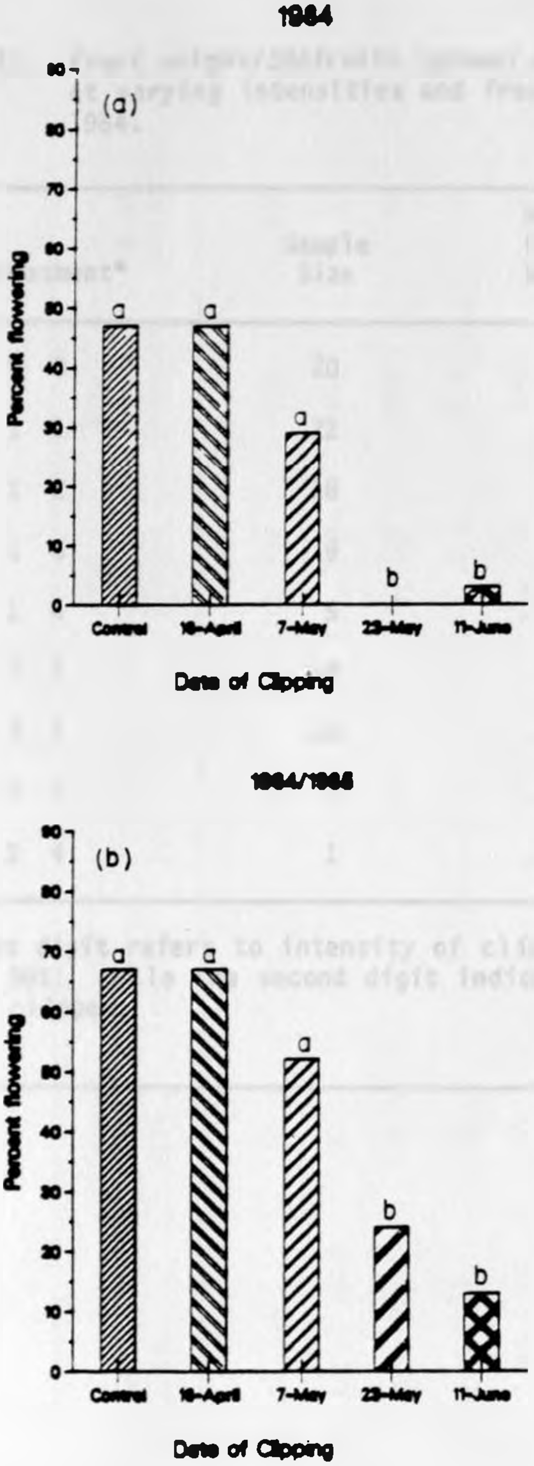


Figure 27. Effect of time of clipping on percent flowering of dyers woad during 1984 (a) and during 1984 and 1985 combined (b). Intensity of clipping and sample size are the same as in Fig. 26. Bars with different letters are significantly different at the 0.05 level.

Table 13. Fruit weight/100fruits (grams) of dyers woad plants clipped at varying intensities and frequencies during the spring of 1984.

Treatment*	Sample Size	Mean Fruit Weight	95% Confidence Limits
0 0	20	.379	.343, .415
1 1	22	.354	.313, .395
1 2	18	.332	.288, .376
1 3	9	.358	.289, .427
1 4	5	.332	.218, .446
2 1	20	.382	.340, .424
2 2	15	.341	.292, .390
2 3	3	.304	.080, .528
2 4	1	.439	-----

*First digit refers to intensity of clipping (0 = Control; 1 = 60%; 2 = 90%), while the second digit indicates number of times a plant was clipped.

Table 14. Fruit production of dyers woad plants clipped* at different dates during the spring of 1984.

Date Clipped	Original Sample Size	Number that Fruited	Mean Fruit Production	95% Confidence Limits	Total Fruit Produced	% of Control
Unclipped	30	20	237	175, 318	4740	100
16 April 1984	30	20	174	123, 234	3480	73
7 May 1984	31	20	100	63, 146	2000	42
23 May 1984	29	7	154	69, 272	1078	23
11 June 1984	30	5	122	31, 272	610	13

*Plants were clipped at 90% of aboveground phytomass.

Table 15. Fruit weight/100fruits (grams) of dyers woad plants clipped* at different dates during the spring of 1984.

Date Clipped*	Sample Size Size	Mean Fruit Weight	95% Confidence Limits
Unclipped	20	.379	.343, .415
16 April 1984	20	.382	.340, .424
7 May 1984	20	.331	.268, .394
23 May 1984	7	.330	.206, .454
11 June 1984	5	.229	.063, .395

*Plants were clipped at 90% of aboveground phytomass.

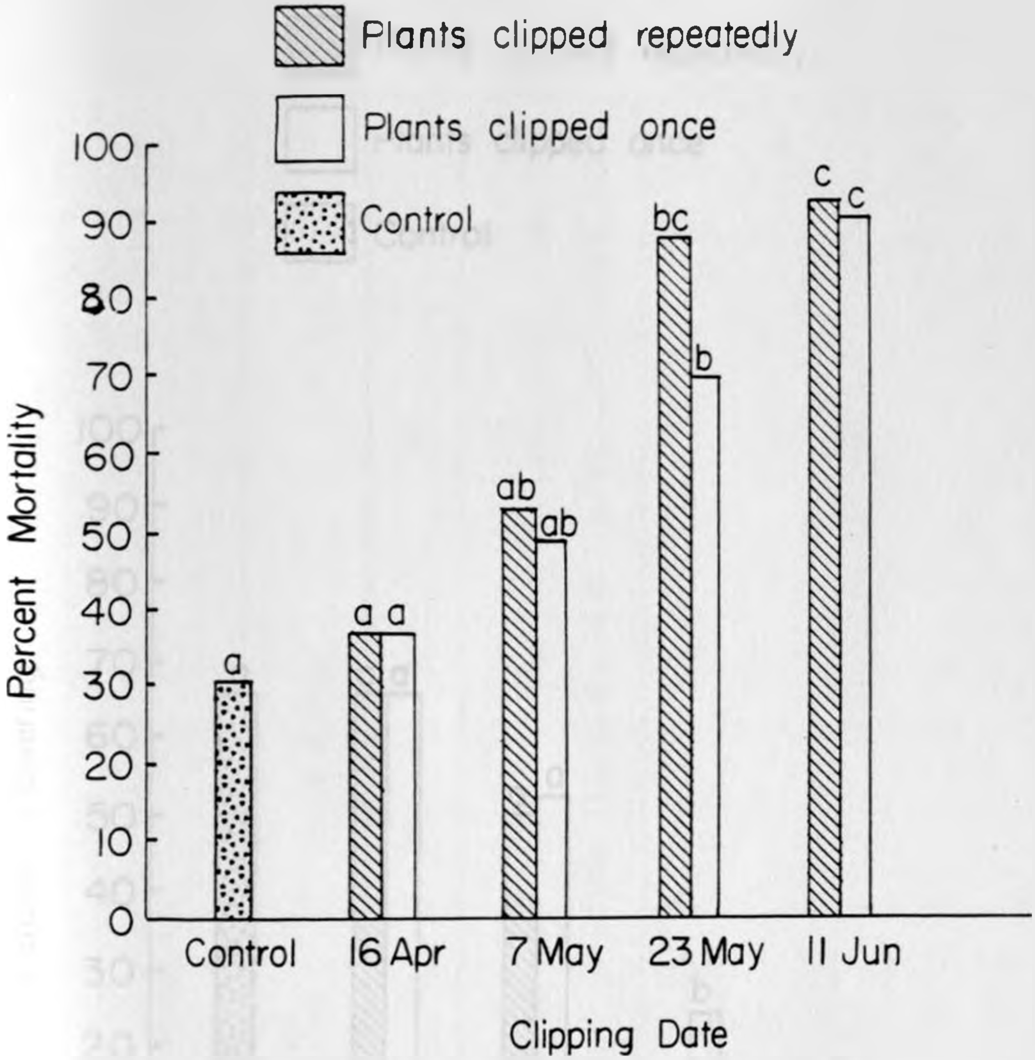


Figure 28. Comparison of effect of multiple clipping and time of clipping on percent mortality of dyers woad during spring/early summer of 1984-1985. Plants were clipped at 90% of aboveground phytomass either repeatedly, on the successive dates, or only once on each date. n = 30 plants. Bars with different letters are significantly different at the 0.05 level.

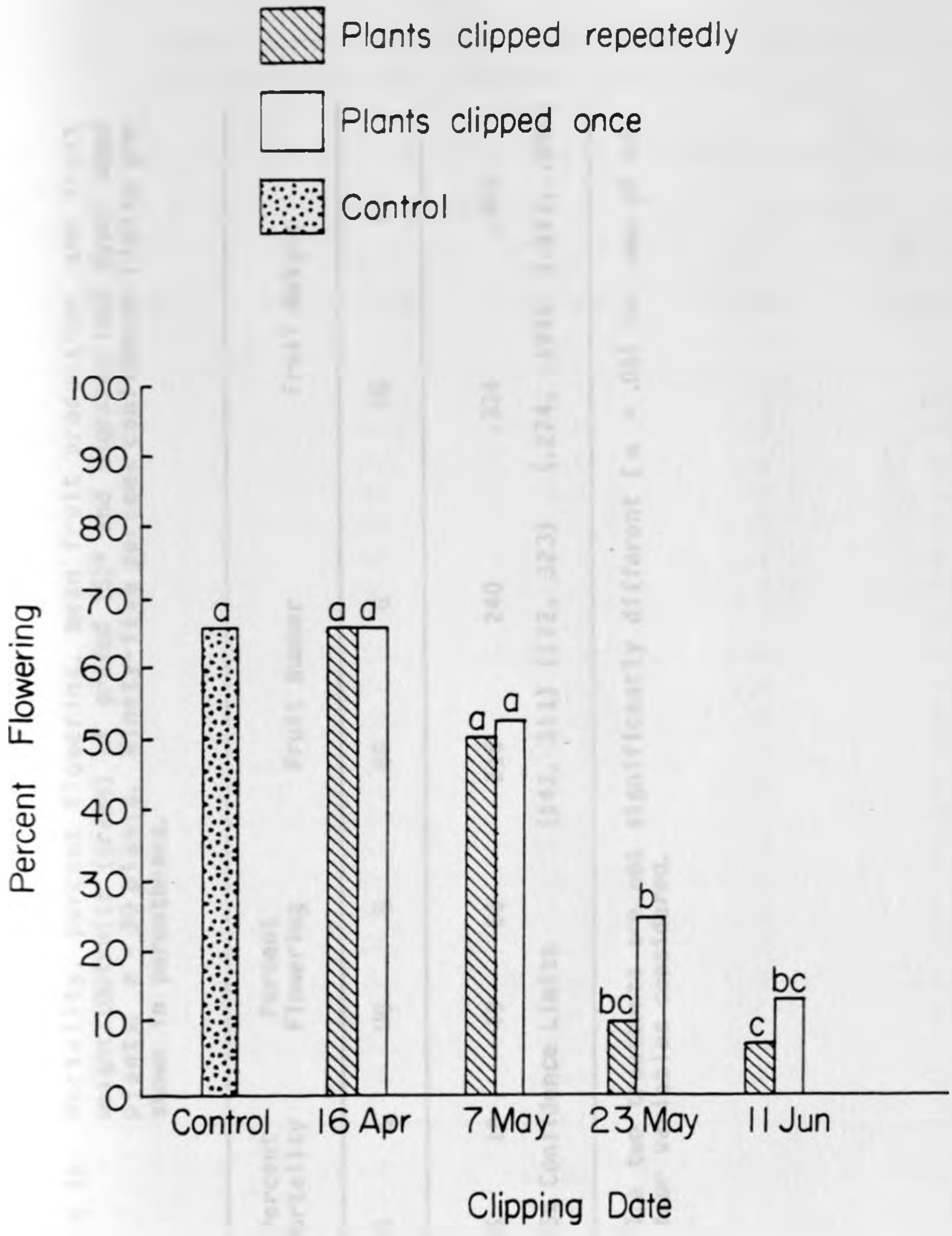


Figure 29. Comparison of effect of multiple clipping and time of clipping on percent flowering of dyers woad during spring/early summer of 1984-1985. Clipping treatments and sample size are the same as in Fig. 29. Bars with different letters are significantly different at the 0.05 level.

Table 16. Mortality, percent flowering, mean fruit production, and fruit weight/100fruits (grams) of grazed (G)* and ungrazed (UG) dyers woad plants. n = 30 plants. Ninety-five percent confidence limits are shown in parentheses.

Percent Mortality		Percent Flowering		Fruit Number		Fruit Weight	
UG	G	UG	G	UG	G	UG	G
25	19	49	51	215	240	.334	.351
95% Confidence Limits				(143, 311)	(172, 323)	(.274, .394)	(.311, .391)

*The two treatments are not significantly different (α = .05) for any of the four variables considered.

Table 17. Basal diameter (cm) and rosette diameter (cm) of grazed and ungrazed dyers woad plants on 18 May 1984.

	Grazed		Ungrazed	
Plant Number	Basal Diameter	Rosette Diameter	Basal Diameter	Rosette Diameter
1	.22	10.7	.43	10.5
2	.45	12.9	.33	10.7
3	.30	8.4	.40	9.0
4	.31	10.9	.25	6.4
5	.45	13.0	.23	7.6
6	.47	13.1	.22	8.1
7	.40	8.0	.35	7.1
8	.80	12.0	.32	7.2
9	.60	12.5	.20	6.1
10	.60	10.5	.35	9.6
11	.30	9.0	.21	6.3
12	.70	14.0	.25	7.5
13	.20	6.0	.40	9.4
14	.30	8.0	.31	9.5
15	.65	14.5	.36	11.1
16	.20	8.0	.20	7.7
17	.60	16.0	.31	8.4
18	.40	11.5	.60	13.4
19	.50	10.0	.60	13.0
20	.70	13.1	.40	8.0
21	.53	9.6	.31	7.0
22	.55	10.9	.40	8.0
$\bar{x}$	.47	11.03	.34	8.71
s.e	.04	.52	.02	.42

grazed plants were greater than those of ungrazed plants (Table 17) suggesting that animals were selecting larger plants. The utilization study was truncated before the end of the growing season since sheep grazing on dyers woad was inconsequential after 18 May 1984. The reasons for the marked switch from grazing on dyers woad can only be speculated upon. The switch could be related to unpalatability, anti-herbivore chemical defenses developed by dyers woad during flowering, and/or may simply be due to availability of other desirable forage at this time of the year.

Discussion of the Grazing Results

As for many other range plant species, clipping damaged dyers woad more severely when it occurred later in the spring. In a single aboveground clipping of dyers woad, Fuller (1985) found that greater mortality and reduced flowering was attained when clipping occurred on 25 June than on 1 May in 1982. Results from the multiple clipping study, and single differentially timed clipping indicate that if plants were clipped on or after 23 May (time of peak bloom), greater mortality and less flowering occurred. Before this date, clipping at 90% of aboveground phytomass twice at two week intervals did not affect survivorship and reproductive capacity of dyers woad. Fuller (1985) demonstrated that to substantially reduce flowering capacity and cause adequate mortality before 23 May, dyers woad had to be clipped 5cm below the ground. This suggests that regeneration of dyers woad, following clipping damage, results from activation of crown buds and those located on the roots just beneath the ground level.

The response of dyers woad to clipping over the spring growing season may be related to the availabilty of soil moisture. Early in the spring growing season, there is probably abundant soil moisture and nutrients within the principal rooting zones allowing regrowth to occur. As the season progresses, soil moisture is depleted and becomes limiting to plant growth (Rawls et al. 1973, West 1983b). Presumably a combination of diminished root absorbing capacity and insuffıcent soil water impeded regrowth of dyers woad from basal meristems following clipping. This would explain the minimal impact of clipping on dyers woad before 23 May, as well as the dramatic effect of a single clipping treatment on or after this date. The role of soil water in plant response to defoliation was demonstrated by Blaisdell and Pechanec (1949) who were able to reverse the adverse effects of clipping on bluebunch wheatgrass (Agropyron spicatum) during the most susceptible period (mid-May to end of June) by watering the plants.

Reproductive loss of dyers woad could come from direct loss of flowering stalks through clipping or may result indirectly from depletion of stored nutrients and carbohydrate reserves or meristematic limitations that are associated with severe defoliation (Trlica 1977, Richards and Caldwell 1985, Archer and Tieszen 1986). The diminished ability of a severely stressed parent plant to support itself or daughter rosettes means that smaller sizes are achieved. This would make reproductive attempts risky.

CHAPTER V

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Livestock grazing, the biological control agency investigated in this study, does not seem to be a feasible method for controlling dyers woad. The intensity and timing of grazing needed to significantly affect its mortality and reproductive capacity will result in range deterioration. The information provided by the associated autecological and population studies of dyers woad will hopefully lead to a more informed approach to its possible control, however.

Population Study

Dyers woad seeds sown in the fall of 1984 germinated both during the fall of 1984 and spring of 1985. Germination from this sowing did not extend past the fall of 1985, however. The rate of germination during the fall of 1984 was less than that observed during spring 1985 and fall 1985. The difference in germination rates between the fall of 1984 and the fall of 1985 could not be correlated with either precipitation amounts or prevailing temperatures. A few of the fruits used to establish the populations were damaged. Seed germination may have been easier from cracked fruits. Differences in germination of freshly sown seeds between fall and spring seasons is consistent with findings of Young and Evans (1971) that dyers woad fruits contain substances capable of inhibiting germination of its own seeds. These as yet unidentified substances are water soluble and therefore leachable. Higher spring germination is thus probably due to more washout of the germination inhibitor. Identification of these substances could provide insight into the manner in which dyers woad invades natural communities. Further studies of the ecology of dyers woad should address this problem.

In the experimentally established populations, individuals germinating during the fall of 1984 overwintered as rosettes twice and then reproduced during the spring of 1986. Individuals germinating during the spring of 1985 overwintered as rosettes only once and the majority of them (87%) flowered and reproduced in the spring of 1986. Thus, on good condition foothill rangelands of northern Utah, dyers woad behaved predominantly as a biennial. However, it has been observed in the clipping study that when mature rosettes and flowering dyers woad plants were subjected to some damage, they were capable of propagating vegetatively, presumably from crown buds.

Similar mortality trends were displayed by fall germinating and spring germinating populations. The highest mortality in both populations coincided with summer drought. The main source of mortality was probably water stress. This could have resulted from inability of the developing root system of the young rosettes to tap the receding soil water during late spring and summer. At the start of the dramatic decline in the two populations (15 June 1985), plants were showing signs of water stress with shrivelled leaves. No evidence of predation or pathogen-induced damage was found on either population.

The fall germinating individuals had bigger rosettes, taller flowering stalks, and more reproductive output than the spring germinating individuals. Fall germination favored both vegetative growth and reproductive capacity measured by fruit production. However, greater germination occurred in the spring.

Dyers woad attained higher germination and establishment rates near sagebrush plants. Plants growing near sagebrush and those in the interspaces, however, did not differ in mortality, vegetative growth and reproductive capacity. The more favorable sagebrush microenvironment (Kline 1973) failed to translate into more vigorous vegetative and reproductive performance of dyers woad. Mortality rates between plants near sagebrush and in the interspaces were comparable despite a seven-fold difference in seedling density. These results have implications for density regulation of dyers woad populations. It can be surmised that density effects were expressed through phenotyptic plasticity and reduced fecundity rather than increased mortality. Manipulative experimentation, where variable densities are established under uniform conditions, would be required to give a better understanding of the role of density in regulation of dyers woad populations.

The population size of dyers woad was constricted at two stages; (i) germination and establishment, and (ii) young rosette. The transition from seed to seedling for the fall germinating and spring germinating populations, when combined, was only .03. The risk of mortality in young rosettes was .77. Mature rosettes had a .81 chance of survival while all bolted individuals reproduced successfully. The population of dyers woad, in terms of fruits, increased by 78% by the end of the life cycle. Within the growing population, young rosettes had the highest risk of mortality. It is suggested that dyers woad be targeted for biological control at this vulnerable stage of growth.

The life-table analysis presented for dyers woad has several limitations that make it inadequate to form the basis of a predictive population growth model. Three crucial elements unaccounted for by the life-table are:

(i) The fate of seeds failing to germinate. Some of these seeds may have undergone enforced dormancy. For purposes of control, it will be imperative to determine seed longevity in the soil under natural field conditions.

(ii) Vegetative reproduction. When damaged, mature rosettes and flowering individuals are known to be capable of reproducing vegetatively from crown buds (King 1966) and root buds (Gilkey 1957, J. O. Evans 1985, pers. comm.).

(iii) Climatic and habitat variability. In this study, dyers woad populations were followed for only two years at one site. Because recruitment, survivorship, and fecundity are likely to be governed by year to year weather patterns (e.g., Klemow and Raynal 1981) and habitat characteristics (e.g., Weller 1985), this type of study should be replicated both in time and space to include the relevant range of abiotic conditions. Transition probabilities derived from such studies can form the basis for matrix modelling of population growth of dyers woad.

Seed Dispersal Study

The seed dispersal pattern of dyers woad was best described by a negative exponential model of the type $\log y = a + bx$; ($r = .78$, $a = 1.92$, $b = -0.02$). Ninety-five percent of the trapped seeds were deposited within 54cm of the parent plants. The greatest recorded distance that seeds moved from their source was 2.4m. The majority of seeds landed on seed traps located to the north and west of the plants, indicating influence of wind direction on local dispersal of dyers woad. These results demonstrate that dyers woad is not commonly spread very far by wind.

The rapid invasion and spread of dyers woad in northern Utah seems to be aided by other forces. The pedicel of dyers woad fruits functions like a hook and can stick to moving objects (e.g., man, livestock and/or wildlife) and thus facilitate animal dispersal. Some plants retain fruits past snowfall. These fruits could be blown over hard packed snow for greater distances. Retention of some fruits also tends to increase the likelihood of deer or birds encountering them and contributing to dispersal. Long range dispersal of dyers woad may also be effected by the action of flowing water. Fruits of dyers woad have flattened wings that would facilitate this mode of dispersal.

The dispersal curve of dyers woad was less steep than that of an inverse square function, indicating that it has the capacity to spread as an isolated colonist (Harper 1977, Watkinson 1978). The dispersal characteristics of dyers woad is hypothesized to be one where the majority of propagules are deposited by wind in a diffused fashion within a few meters of parent plants, while a small proportion is carried for long distance with the aid of man, wildlife, and water.

Root Study

The root system of dyers woad was predominantly a taproot with some laterals in the upper 30cm of the soil. Little difference was found between the mapped taproot length and total mapped root length of mature plants and rosette plants. A significant interaction effect between plant category and soil rooting depth indicated that rooting pattern varied with plant category. Mature plants had greater root length in the upper 20cm of the soil, with 43% occurring in this soil layer. In the rosette plants 31% was found in this layer. Lateral branching near the soil surface may occur during the second year of growth since mature individuals showed the most marked branching in the upper 20cm of the soil.

The rooting pattern of dyers woad is probably suited to Intermountain environments. Maximum soil moisture accumulation in mid-winter/early spring is typically followed by a warm growing season with little precipitation (West 1983b). The lateral roots near the soil surface can exploit moisture from slowly melting snow during early spring while taking advantage of any summer precipitation. The deeper taproots may, in turn, allow utilization of water lying below the principal rooting zones of associated herbaceous species. Dyers woad seems to have a rooting pattern similar to that of sagebrush, a pattern postulated to confer a strong competitive ability in the semi-desert steppe of the Intermountain West (Sturges 1977).

It is suggested that further work on rooting characteristics of dyers woad focus on phenology as it relates to the timing of root growth over winter and early spring. If as in cheatgrass (Bromus tectorum), dyers woad is capable of root growth under low temperatures during winter and early spring (Harris 1967, 1977), then it would be expected to extract soil moisture and nutrients at higher rates than native grasses during the earlier part of the spring growing season.

Clipping and Utilization Studies

The response of dyers woad to clipping indicated that a single, late spring clipping, at 90% intensity, caused similar impacts on mortality and flowering as multiple clipping at the same intensity. Significant mortality and reduction in percent flowering was achieved only when clipping occurred on or after 23 May 1984. It can be concluded that, in restricting dyers woad, time of clipping is more crucial than number of times clipping occurs during spring. These results were interpreted to mean that clipping response of dyers woad may be dependent on declining soil moisture availability over the growing season.

A study of dyers woad utilization by sheep showed that these animals switched to other forages by 18 May, three weeks after grazing began on the pasture. During this period, only 16% of the monitored plants had some utilization. The average degree of utilization on grazed plants was 39% of aboveground tissue removed. This level of utilization did not have any significant effect on mortality, percent flowering, and fruit production of dyers woad. The basal diameter and rosette diameter of grazed plants were greater than those of ungrazed plants suggesting that animals were selecting larger individuals.

Grazing on dyers woad does not come at a time during which much impact on mortality or seed production can be attained. Significant mortality and reduction in seed production of dyers woad occurs only by grazing late in spring (on or after 23 May in 1984). This is the time of the year when other forages are available. Sheep will not voluntarily utilize great amounts of dyers woad. Furthermore, desirable perennial grasses and forbs (e.g., _Agropyron spicatum_ and _Balsamorhiza sagittata_) that are associated with this weed are susceptible to heavy grazing at this time of the year (Stoddart 1946, Blaisdell and Pechanec 1949). Therefore, the stocking required to restrict dyers woad will result in range deterioration. Sheep grazing concentrates on larger dyers woad plants. Survivorship of these plants is high. They are also capable of vegetative reproduction. Livestock grazing is, therefore, an inappropriate biological means for controlling dyers woad if management goals include sustained range condition. The results of the clipping and utilization studies do not corroborate observations by some graziers and Parker (1980), that grazing reduces dyers woad populations. This apparent contradiction may be due to: (i) the clipping and utilization experiments occurred within one spring season and, therefore, did not simulate repeated grazing over several years and, (ii) defoliation delays flowering of dyers woad (Fig. 27a and b; Fuller 1985). Since dyers woad is most conspicuous at the flowering stage, lack of flowering may be mistaken for absence of the woad plant.

More host-specific biological agents should be tried for controlling dyers woad on Utah rangelands and those of surrounding states. It is imperative that such biological control agents cause maximum damage on young rosettes since it is at this stage that dyers woad is most susceptible to mortality. Greater overall control of dyers woad might be realized through an integrated approach by combining biological control efforts with the use of highly selective herbicides, e.g., those which would prevent formation of viable seeds. Unless there are some unanticipated developments, dyers woad will probably continue to increase in density where it now occurs and spread more widely in the Intermountain West.

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