

**LONG-TERM SAGEBRUSH
POPULATION DYNAMICS
AND UNGULATE USE AT SELECTED
LOCATIONS ON THE NORTHERN RANGE OF
YELLOWSTONE NATIONAL PARK**

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ABSTRACT: To assess long-term effects of ungulate use on sagebrush (*Artemisia tridentata*) 5 locations on the northern range of Yellowstone National Park were chosen for the establishment of 2ha ungulate exclosures in 1958 and 1962. Sagebrush belts (1.524m wide and either 15.4m or 30.4m long) were placed inside and outside the exclosures on similar sites when the exclosures were established. Sagebrush canopy coverages were mapped to their exact location within each of the belts starting with the establishment of the belts and continuing with each resurvey conducted in 1962, 1967, 1974, 1981, 1986, and 1989. From the mapped canopy coverages the total amount of sagebrush canopy coverage per belt was calculated along with these demographic characteristics: number of individual sagebrush, size distribution of individual canopies, survival, recruitment, turnover, and longevity of sagebrush. The total amount of canopy coverage in an area was analyzed with repeated measures multivariate analysis. Rates of sagebrush canopy coverage growth did not statistically differ between inside and outside of the exclosures. Rates of growth did statistically differ between locations on the northern range and for the interaction of growth rates between locations and inside and outside exclosures. The significant interaction was reflected in that 3 of the 5 locations had rates of canopy coverage growth much higher inside the exclosure than outside, and ungulate use of sagebrush outside was suggested as the reason for the difference. Ungulate use was also responsible for differences in demographic patterns in 2 of the locations. Demographic patterns differed between locations ranging from 1 exclosure at a self-thinning and density-dependence stage, to the other locations and exclosures at stages which are controlled by stochastic environmental factors and the interaction of sagebrush and ungulate use. The differences in location responses leads us to believe that each location or patch has its own location-specific sagebrush dynamics. Assessments of sagebrush condition now or in the future depend on knowing the dynamic state of a majority of patches on the northern range.

INTRODUCTION

Sagebrush (*Artemisia tridentata*) is the dominant plant of the sagebrush steppe on the northern range of Yellowstone National Park (Beetle and Johnson 1982, Houston 1982). The sagebrush steppe constitutes approximately 22% of the northern range area. Sagebrush plays an important role in the functioning and dynamics of plant communities (Beetle and Johnson 1982, West 1983), in nutrient cycling (Burke 1989), fires, and ecosystem dynamics (West 1983). Sagebrush is important in the relations of ungulates on the northern range (Houston 1982, Singer 1991a). The northern range is the major wintering area for the majority of Yellowstone's resident elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and the Lamar herd of bison (*Bison bison*) (Houston 1982). All of these aspects point to sagebrush as being one of the most important biotic entities on the Northern Range.

With sagebrush being such a dominant plant and important to the northern range ecosystem functioning and processes, knowledge of the long-term dynamics of sagebrush would be of importance to any manager concerned with the northern range ecology (Coughenour and Singer 1991). To study the long-term dynamics of sagebrush under ungulate use was one of the motivations in the establishment of ungulate exclosures in 1958. The exclosures (2ha in size) were designed to exclude all ungulates. To study the long-term aspects of sagebrush canopy coverage and demographics (demographics being number of individuals, mortality, recruitment, size distribution of individual plants, and longevity of sagebrush), permanent belt transects were established both inside and outside the exclosures. Measurements taken at the belt transects were locations of sagebrush and canopy coverage of individual sagebrush. Since their initiation the belts have been resurveyed every 4 to 7 years.

The exclosures resulted in a treatment where ungulates have been excluded from inside the exclosure for approximately 32 years. The purpose of the study is to contrast the enclosed sagebrush in the exclosure with sagebrush outside the exclosure. The sagebrush inside the exclosure will be further referred to as Enclosed and those outside as Open. We compared sagebrush canopy coverage and demographics in Enclosed and Open treatments identifying differences which resulted from the lack of ungulate use and suggested possible explanations for the differences. Other objectives were as follows: 1) compare the patterns of sagebrush demographics inside and outside the exclosures, and suggest what processes are responsible for the observed differences, 2) assess the status of the sagebrush populations on the northern range speculating as to the continued persistence of sagebrush, i.e., the ability of sagebrush to persist on the northern range given that environmental conditions do not change drastically from the last 30 years, and 3) develop a case for how the sagebrush populations relate to patch and landscape scale dynamics.

STUDY SITE AND METHODS

The study was conducted on the northern range of Yellowstone National Park as described by Barmore (1980) and Houston (1982). The northern range lies in the northern 1/3 of Yellowstone National Park along the Yellowstone and Lamar rivers. The climate of Yellowstone National Park is generally cool and wet, but lower elevation sites are drier and hotter than those at a higher elevation. Climate data are reported by Singer (1991b) and by Reardon (1991). The vegetation of the northern range is composed of grasslands, sagebrush steppes, and coniferous forests and has been described by others (Barmore 1980, Houston 1982).

In 1958 one enclosure 2ha in size was built at each of 4 different locations on the northern range: Gardiner, Mammoth, Blacktail, and Lamar (Fig. 1). The enclosures were intended to exclude all large ungulates from the area in order to study the effects of the ungulates on the vegetation. In 1962 an additional location had an enclosure built on it, Junction Butte, with second enclosures built in 1962 at Gardiner and Blacktail. A second enclosure was built at the Lamar location but was not included in this study because the second enclosure was 2 miles from the original enclosure location and was felt not to be similar to the conditions in the 1958 enclosure. Enclosure locations were selected to represent areas of known elk use and where elk use was thought to be heavy (Barmore 1980, Houston 1982).

The Gardiner location lies in the "Boundary Line Area" (Houston 1982) which was added to the park in 1932. Prior to its acquisition by the park the location was subject to heavy livestock use throughout the year (Houston 1982). The enclosure, located on an old landslide deposit, has had the soils and vegetation described by Singer (1991b) and Lane (1990). It occurs at about 1,615m in elevation and is dryer and hotter than the other locations. The sagebrush present on this site is Wyoming big sagebrush (*A. tridentata* subsp. *wyomingensis*) which is adapted to xeric sites (Beetle and Johnson 1982, Barker and McKell 1983). The other locations are on glacial till composed of recent volcanics, granitic and sedimentary rocks. These locations are at higher elevations (1,920 to 2,042m) than Gardiner and are cooler and wetter than Gardiner. The soils and vegetation have been described by Singer (1991b) and Lane (1990). The sagebrush found on the sites are mountain big sagebrush (*A. tridentata* subsp. *vaseyana*) and basin big sagebrush (*A. tridentata* subsp. *tridentata*) with only scattered individuals of basin big sagebrush present at any of the locations.

Data Collection

To assess the long-term dynamics of sagebrush at each enclosure location, permanent belt transects were established. Each belt was 1.524m wide and either 15.24m or 30.48m long. The shorter belts were established at Mammoth and Lamar. Belts were paired with one inside and another outside the enclosures. The areas where belts were located were consciously selected to be as similar as possible within a location and had to have sagebrush present on them (Barmore 1980). At Gardiner the belts were placed on flat to gently sloping terrain which has a variable microtopography due to the landslide characteristics upon which the belts were placed. The belts at Mammoth and Junction Butte are on flat ground with the Junction Butte belts having a large amount of microtopography and small-scale soil differences (Lane 1990).

The Blacktail belts are on 20% south facing slopes with the belts going from the toe slope up. At Lamar the belts were placed on 30% south facing slopes with the belts going from the toe slope up. Sites selected for belt placement inside the 1962 Blacktail and Gardiner enclosures were designed to be as similar as to the sites selected for belts in 1958.

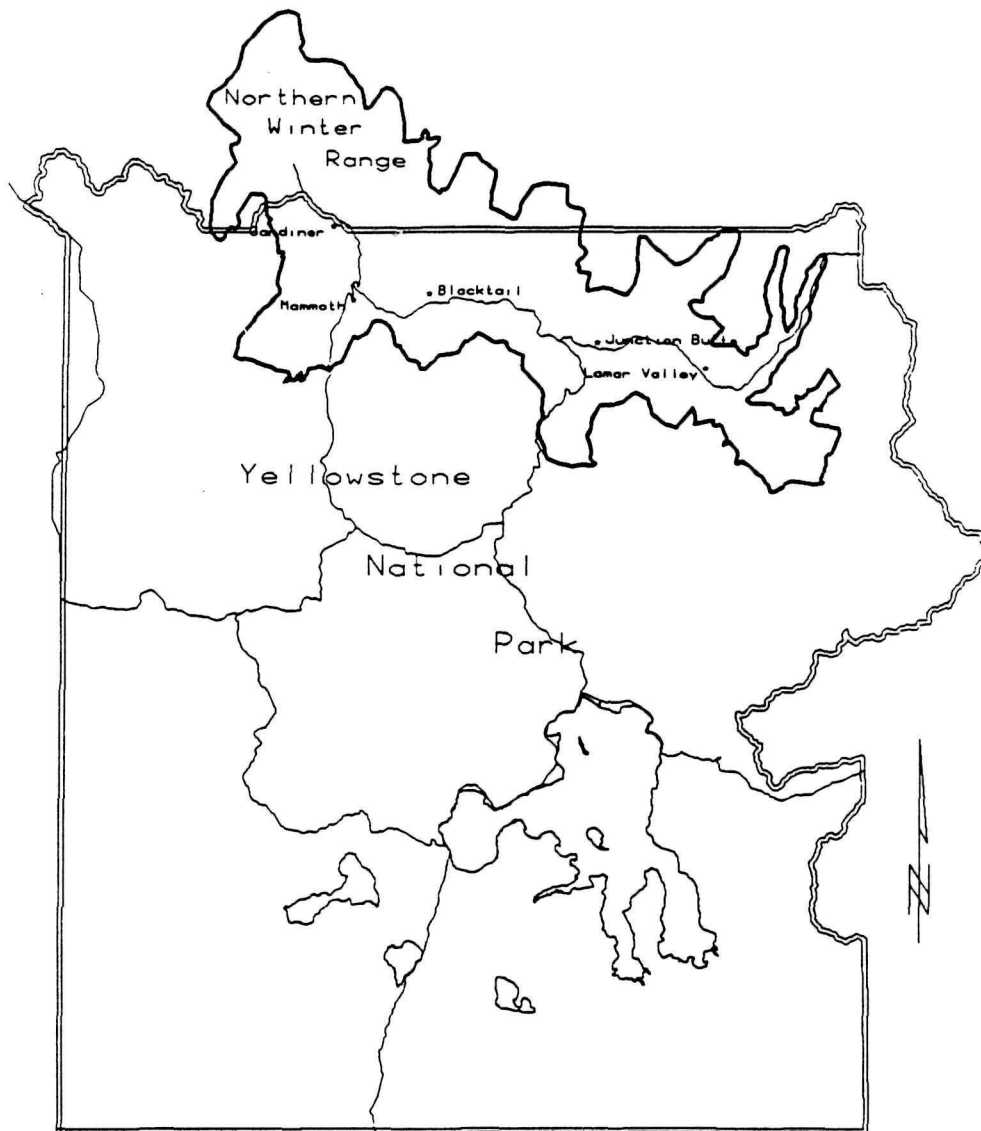


Fig. 1. Exclosures at 4 different locations on the Northern Range: Gardiner, Mammoth, Blacktail, and Lamar.

Data collection on sagebrush in the belts consisted of mapping the outline of each individual green sagebrush canopy to scale on a piece of paper for each survey. The belts were surveyed midsummer. Every sagebrush taller than 10cm was mapped to the exact canopy coverage and position it occupied on the belt. Areas of canopies were calculated by either planimeter or by using area grids. Locations of individual sagebrush were marked and followed over time recording when they appeared in the belt through recruitment and when they disappeared through mortality. In the 1958, 1962, 1967, 1986, and 1990 surveys, the individual outline of each green sagebrush canopy was recorded. For these surveys and the intervals between, canopy coverage, number of individuals, survival, and recruitment were determined. For the 1974 and 1981 surveys, the outlines of individual sagebrush were lumped together so only canopy coverage and survival of sagebrush could be determined. Recruitment rates and measurements based on individuals were not possible for these 2 survey years. For the Enclosed Belt at Junction Butte, the 1967 survey had the outlines for individual shrubs combined together and was not analyzed on an individual basis. In the analyses where individual shrubs were used, those individual shrubs not rooted inside the belt were excluded from the analysis. For the sake of comparison, all data were scaled to the longest length (30.48m) and largest area (46.5m²) of the belts.

Neither were all the belts started at the same time nor were the surveys conducted over the same time period. The Junction Butte belts were started in 1962 at the same time that belts in the second exclosures at Gardiner and Blacktail were started. The belts at Lamar were not surveyed in 1986. The Blacktail belts were completely burned in 1988 and all sagebrush was consumed.

Analysis of Canopy Coverage

Analysis of sagebrush canopy coverage between the treatments was done using repeated measures multivariate analysis. Canopy coverage here is the total coverage by sagebrush irrespective of individuals. In those situations where overlap between individuals occurred, only the area of the overlap was used in the analysis, not the sum of areas from each individual overlap. Because of the sequential measurement of the same piece of ground (belt) over time, the amount of canopy coverage from one survey to the next was considered correlated. Repeated measures is the preferred method for analyzing correlated, longitudinal studies (Potvin et al. 1990, Eberhardt and Thomas 1991). To provide some measurement of within location error, the belts were broken into 10 4.65m² blocks on the longer belts or 5 blocks for the shorter belts. The canopy coverage in each block then becomes the response variable. Each block acts as a subsample within the locations with each of the 5 locations being replicates. The blocks were not tested for normality of errors, but were logarithmically transformed as suggested by Eberhardt and Thomas (1991). The use of this transformation is common when data are sequential and based on growth. Because repeated measures analysis is sensitive to unbalanced designs, the analysis was conducted on data from survey years 1962, 1967, 1974, 1981, and 1986. The surveys done in 1958 were not included, because not all locations had data from that survey (Junction Butte was only started in 1962), and the 1990 surveys were not included because Blacktail had burned in 1988. The exclosures at Gardiner and Blacktail in 1962 were not included because they created an unbalanced design. Missing values for the 1986 survey at Lamar were estimated as the midpoint between values of sagebrush canopy coverage found in the 1974 and 1990 surveys.

In the repeated measures analysis the ungulate use treatments were considered one grouping factor and the 5 locations were treated as another grouping factor. The repeated measurements of each block's canopy coverage for each successive survey were referred to as the trials factors. The analysis tests whether the grouping factors are different in 2 ways: 1) to test the between subjects effects which ignores the correlations and variance among the trials factors using only the summed values of all the trials factors within a block, and 2) to test the within subjects effects by linearly transforming the trials factors and contrasting the different grouping factors. The between subject effects tests result in tests similar to that found by doing a 2-way ANOVA test on the means of the groupings while the within subjects effects is a test of the interaction of the trials factors on the groupings. Significance found in the within subject effects of either grouping factor is evidence that the linear response of the trials factors is different between the groups.

Interaction found in the within subject effects between the grouping factors suggests that the linear response between the grouping factors is different for various combinations of the grouping factors. The multivariate model that tests the within subjects effects for repeated measures was chosen over the univariate model because of its less stringent assumptions on the form of the covariance matrix (Potvin et al. 1990). The multivariate statistic Pillai's trace is the only reported statistic and is recommended by Potvin et al. (1990) for the combination of sample size, number of trials factors, and number of groups found in this design. The tests for compound symmetry of the covariance matrix, along with the homogeneity of the variance-covariance matrices, were not done because of the small number of samples and the fact that the results from tests on such small samples may be unreliable.

Analysis of Demographic Characteristics

The analysis of demographic characteristics was conducted on information from the whole belt. The small blocks were not used because the blocks provided insufficient size to characterize the demographic variables. Because the analysis was conducted on the belts there were insufficient samples for many statistical tests to be conducted. Instead, comparisons between the treatments utilized indices and graphical means. Survival was tested between the treatments.

Size Distribution.--The size distribution of individual sagebrush canopies was one of the demographic characteristics measured. Knox et al. (1989) found that the size structure of a population of plants can be used as a statistical bridge from individual to population level effects, and can be used to infer about past or present competitive environments within that population. To analyze the size distribution, canopies were classified into 4 classes: 1) 0.0001m^2 to 0.037m^2 , 2) 0.0371m^2 to 0.11m^2 , 3) 0.111m^2 to 0.37m^2 , 4) 0.371m^2 to 1m^2 . The smallest class was composed of immature individuals (sagebrush plants which had not flowered), though some individuals were up to 24 years old. The larger classes were composed of mature plants in different stages of development. To further analyze the distribution of canopy sizes, the degree of size hierarchy among the distributions were calculated using the Gini (G) coefficient. The Gini coefficient is an index (Wiener and Solberg 1984) used to measure the amount of hierarchy in a distribution. The Gini coefficient values increase when the proportion of individual canopy sizes are distributed unequally among the size classes. The more unequal the distribution the higher the Gini coefficient. The Gini coefficient runs from zero to 1 with zero meaning that all classes are equal. The Gini coefficient has been recommended by Knox et al. (1989) to analyze patterns of distributions in plant demographics.

Recruitment, Mortality, and Turnover.--Recruitment and mortality were measured for the sagebrush in enclosed and open belts. Recruitment was the number of new individuals entering a size class. Mortality is the number of individuals which were no longer present on the belt since the last reading of the belt. A different classification of individual sagebrush canopies was developed to help in the analysis of recruitment, mortality, and turnover patterns. Canopies were divided into only 2 classes to simplify analysis. Canopies from $>0\text{m}^2$ to 0.037m^2 were classified as the Immature Category (though as stated earlier this did include some older aged individuals), and canopies from 0.0725m^2 to 0.55m^2 were classified as the Large Category. Survival of sagebrush was tested using techniques outlined by White (1983) and program SURVIV (Owens and Norton 1990). The survival of individuals in size classes in the various finite periods between surveys was tested between Enclosed and Open Belts. Significance was found if the log-likelihood ratio of the full model (survival is independent over periods between belts) to the constrained model (survival is the same over the periods for belts) was found significantly different.

Turnover Rate (the percentage of new individuals in the population) was calculated for the full length of study for each belt. Average yearly Turnover Rate (T) is defined as:

Where m is the cumulative mortality for the belt for the length of the study, r is the cumulative recruitment, y is the number of years that the belt was studied, d_1 is the number of sagebrush individuals at the start of

$$T \text{ per year} = \frac{((m+r)/2)/y}{(d_1+d_y)/2}$$

the belt, and d_y is the number of sagebrush individuals at the end of the study.

Because the data were collected by various researchers there is a lack of continuity. This lack of continuity gives rise to questions about the accuracy of the mapping. Instances could have happened where inaccurate mapping from one period to the next could cause an established plant's locations to be moved. This movement would result in the interpretation that there is a new plant at the inaccurate location and that the old plant at the original location had died. This type of error was probably not prevalent, since instructions from the beginning of the study were to map sagebrush canopies onto grids 1ft apart and to take care in locating each sagebrush canopy on the grid. The few errors that probably did occur would bias downward the estimates of longevity and increase estimates of mortality and recruitment. Another source of error was that an individual would die before the next survey and be replaced by another, so that the death and recruitment of the individuals would not be recorded. This error was controllable because the sudden decrease in size of an individual sagebrush would be noticed, and this decrease in size would be interpreted as a new plant.

RESULTS

The results of the repeated measures analysis (Table 1) are split into 2 different analyses: 1) Between Subjects Effects, and 2) Within Subjects Effects. The Between Subject Effects analysis ignores the correlated structure of the repeated measurements on the belts (blocks) over time. Essentially this results in a test of group means averaged over all the surveys. Because the belts probably differed statistically in the amount of canopy coverage when they were first established, a test of the location of the averaged group means is not informative because there was already a significant difference in the groups means inherent in the data. Such a test would not help in establishing if there was a difference in the response of the sagebrush canopy coverage among the treatments. The tests in the Within Subjects Effects were different from the Between Subjects Effects in that the rates of canopy coverage growth are compared. The tests of the rates of growth ignore location, and only look at rates, thus even if the belts do start out different, the rates of growth should only be responsive to the Treatment Effects and not reflective of some pretreatment difference. The Within Subject Effects test is the best indicator if there has been a difference in the response of sagebrush canopy coverage among the treatments.

The Between Subjects Effects tests of the ungulate use treatment and location found sagebrush canopy coverage on the 4.6m² plots significantly different between locations ($P = 0.014$) and between Enclosed and Open Belts ($P < 0.0001$). Interaction between location and the ungulate use treatment was found to be significant ($P = 0.021$). Results of the Within Subjects Effects found no significant difference between Enclosed and Open Belts (Pillai Trace $P = 0.063$). Tests of location effect was significantly different (Pillai Trace $P = 0.031$), and interaction between location and treatment was significantly different (Pillai Trace $P = 0.031$). The interaction between location and the Ungulate Use Treatment in the response of the rate of canopy coverage growth is evident in Fig. 2 with both the Gardiner and Mammoth Enclosed Belts having higher growth rates than the Open, while Blacktail and Junction Butte differed little. The 1962 Enclosed Belts at Blacktail and Gardiner show the same trend, even though these belts started at a different time.

Table 1. ANOVA table for the repeated measures multivariate analysis of variance tests on sagebrush canopy coverage for the ungulate use treatment and location. Effects are separated as (A) between subjects and (B) within subjects.

A) Between Subjects				
Sources	MS	<i>F</i>	<i>df</i>	<i>P</i>
Treatment	134.9	14.17	1	0.000
Location	31.8	3.35	4	0.014
Interaction	29.4	3.09	4	0.021
Error	9.517		70	
B) Within subjects				
Sources	Pillai's Trace	<i>F</i>	<i>df</i>	<i>P</i>
Trials effect	0.615	26.7	4, 67	0.000
Treatment	0.123	2.3	4, 67	0.063
Location	0.373	1.7	16, 280	0.031
Interaction	0.386	1.8	16, 280	0.023

Testing the sagebrush canopy coverage of just the Enclosed Belts in repeated measures analysis found that the Between Subject Effects for locations were significantly different ($P = 0.02$). This indicates that the amount of sagebrush canopy coverage is different among the locations. The results of the Within Subjects Effects for location finds that the rate of growth in sagebrush canopy coverage was not significantly different (Pillai's Trace, $P = 0.563$).

The Lamar location does differ in its growth rate between Enclosed and Open Belts (Fig. 2). This difference may be more reflective of disturbance rather than the treatment effect. The Open and Enclosed sites are on steep southerly exposures which are easily disturbed because of their slope and aspect. This disturbance may account for the Open Belt having started with a low sagebrush canopy coverage and having a slow growth rate. Because of the potential for disturbance on the belts, the comparisons between the Ungulate Use Treatments tend to be weak which leads us to drop any further analyses of the Lamar location.

Demographic Characteristics

Because the interaction between locations and the ungulate use treatment was found to be significant for sagebrush canopy coverage, we conclude that the locations were responding differently to the Ungulate Use Treatment. Therefore, results and inferences of the patterns of sagebrush demographics will be restricted to each location. The results from the locations were contrasted together to establish difference of locations.

Gardiner.--At the Gardiner location both total canopy coverage and number of individuals increased in the Enclosed Belts while on the Open Belt they stayed the same or decreased (Fig. 3). The number of individuals in the larger size classes increased in the Enclosed Belts resulting in larger Gini coefficients while no increase was seen in the Open Belt. Survival was significantly higher for the 1958 Enclosed cohort than for the 1958 Open cohort for the smallest size class ($P < 0.0001$) (Fig. 4). Survival was not tested for the other cohort years because of small sample size. The Open belt had very few individuals left on it by the last survey with only 2 in the large category. Cumulative large category mortality and recruitment were reversed in the Open to the Enclosed Belts with the Open Belt having more mortality than recruitment in the large category. Five year turnover rates ranged from 18.67 to 24.6 with no real difference between Open and Enclosed Belts and between all sizes of plants (Table 2).

Table 2. Five year turnover rate, percentage of sagebrush plants that are new, from the beginning to last survey of each belt. Turnover rate given for all categories of sizes, overall, and just for the large category, large.

Location	Overall		Large	
	Enclosed	Open	Enclosed	Open
Blacktail 58	20.83	20.58	29.51	32.42
Blacktail 62	22.19		13.88	
Gardiner 58	19.79	19.58	18.67	22.56
Gardiner 62	24.6		19.9	
Junction Butte 62	20.98	17.48	26.78	17.85
Mammoth 58	35.76	21.28	37.59	25.17

Mammoth.--At the Mammoth location total canopy coverage increased and number of individuals decreased in both the Enclosed and Open Belt (Fig. 3). Mammoth had the highest canopy coverage (50%) for a belt in comparison with the other locations and had the highest numbers of individuals (5.9 plants per 46.6 m²). The number of individuals in the larger size classes increased in both belts, but the numbers in the small size class decreased in the enclosed. This reduction in small class numbers for the Enclosed Belt results in a decreasing Gini coefficient because of the decrease in inequality between the distribution classes while in the Open Belt the small size class contained proportionately more individuals than the other classes resulting in an increasing Gini coefficient. Survival for the 1958 Enclosed cohort was significantly higher than the 1958 Open cohort for the smallest size class ($P < 0.0001$) (Fig. 4). Survival was not tested for the other cohort years because of small sample size. For both belts recruitment exceeded mortality in the large category. Five year turnover rates ranged from 21.28 to 37.59 with higher rates in the Enclosed Belt and no difference between sizes of plants (Table 2). Mammoth had the highest turnover rates compared to the other locations.

Blacktail.--At the Blacktail location total canopy coverage increased on all belts while number of individuals decreased in the Open Belt and stayed the same in the Enclosed Belts (Fig. 3). The number of individuals in the larger size classes increased in all belts, but the small class had proportionately more individuals compared with the larger classes.

The Gini coefficient increased on all belts. Survival was significantly higher for the 1958 Enclosed cohort than for the 1958 Open Belt cohort for the smallest size class ($P < 0.0001$), but not significant for the 1962 cohort year ($P = 0.158$) and 1967 cohort year ($P = 0.483$) (Fig. 4). A test of the overall survival using methods outlined by Rice (1990) found that survival for the smallest size class was significantly different between Enclosed and Open Belts ($P = 0.0029$). Survival was not tested for the other cohort years because of small sample size. For all belts recruitment exceeded mortality in the large category. Five year turnover rates ranged from 13.88 to 32.42 with no difference between Enclosed and Open Belts and a variable response in the differences between size classes (Table 2).

Table 3. Percentage of individuals from different cohort years contributing to the last survey of individuals in the large size category (0.0725 m² to 0.55 m²). Number of individuals in parentheses.

Location	Percent of Individuals From Cohort Year				
	1958	1962	1967	1986	1990
Blacktail Enclosed 58	37.2 (16)	0 (0)	11.6(5)	51.2 (22)	
Blacktail Open 58	23.3 (7)	6.7 (2)	10 (3)	60 (18)	
Blacktail Enclosed 62		50 (6)	25 (3)	25 (3)	
Gardiner Enclosed 58	32.1 (9)	10.7 (3)	7.1 (2)	42.8 (12)	7.1 (2)
Gardiner Open 58	50 (1)	0 (0)	50 (1)	0 (0)	0 (0)
Gardiner Enclosed 62		10 (6)	0 (0)	80 (48)	10 (6)
Junction Butte Enclosed 62		0 (0)	0 (0)	88.9 (8)	11.1 (1)
Junction Butte Open 62		44 (11)	16 (4)	28 (7)	12 (3)
Mammoth Enclosed 58	7.7 (2)	0 (0)	0(0)	61.5 (16)	30.8 (8)
Mammoth Open 58	13.3 (2)	0 (0)	0 (0)	80 (12)	6.7 (1)

Junction Butte.--At the Junction Butte location total canopy coverage increased on both belts while number of individuals decreased in the Open Belt and stayed the same in the Enclosed Belt (Fig. 3). The number of individuals in the larger size classes increased in all belts, but the small class had proportionately more individuals compared with the larger classes. The Gini coefficient increased on all belts. Survival was significantly higher for the 1962 Open cohort than for the 1962 Enclosed cohort for the smallest size class ($P = 0.0029$) (Fig. 4). Survival was not tested for the other cohort years because of small sample size. For all belts recruitment exceeded mortality in the large category. Five year turnover rates ranged from 17.48 to 26.78 with the Enclosed belts having a higher turnover though there was no difference in the size class turnover rates (Table 2).

Turnover Rate.--The calculated level of turnover indicates that after 25 years enough sagebrush mortality and recruitment have occurred so that the sagebrush population should be composed of all new individuals. The actual composition of individuals contributing to the population on the last survey for the large category shows that a percentage of plants persisted from the start of the belts (Table 3) with individuals from other years contributing. The contradiction between the longevity of certain sagebrush and the high turnover rate is a result of the fact that the turnover rate does not take into account the longevity of sagebrush but just looks at the ratio of mortality to recruitment. Thus these sagebrush populations are characterized by a minority of long-lived sagebrush which are far outnumbered by the majority of short-lived sagebrush which come and go in a 25-year period.

DISCUSSION

The early surveys (1958 and 1962) show that all the belts were at low sagebrush canopy coverage levels. The majority of individual canopies were found in the smallest size classes with few if any in the larger classes. This pattern is representative of a sagebrush population which is starting to develop. Disturbances that can cause sagebrush to be at early development levels are: 1) fire, 2) extended drought (West et al. 1979, Young et al. 1989), 3) pathogens (Nelson and Sturges 1986, Nelson et al. 1990), 4) winter mortality (Hanson et al.

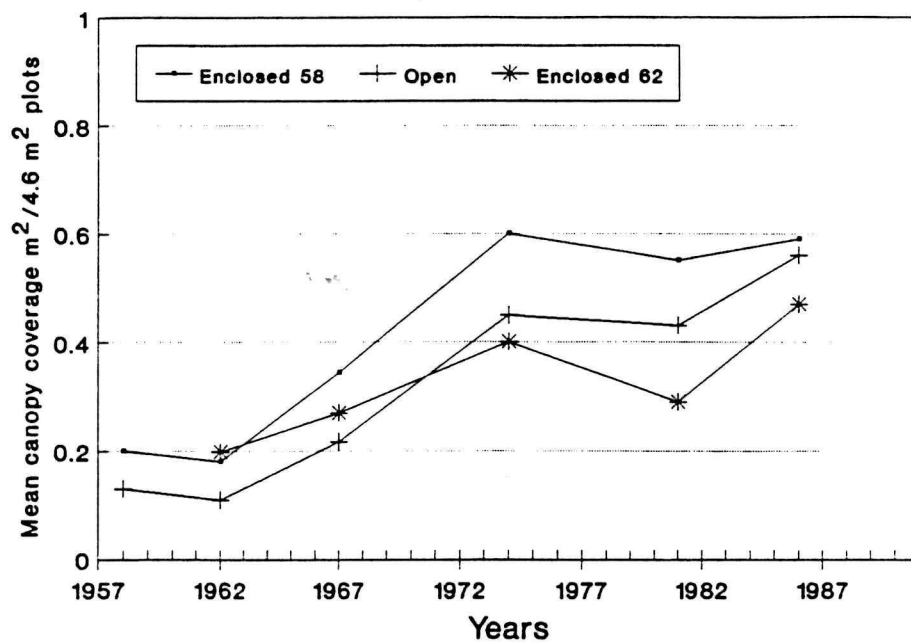
1982), 5) root flooding (Ganskopp 1986, Weber 1990), and 6) herbivory (West 1983). It is unknown if any or all of these factors were responsible for the sagebrush at the early stages of development (Barmore 1980; Houston 1982; Don Despain, pers. commun.; Mary Meagher, pers. commun.). It is unknown how long ago such disturbances might have occurred, but fire at all locations has not been recorded since 1930, except for Blacktail which burned in 1988.

The locations differed in the amount of sagebrush canopy supported in the belts. The differences between locations can be caused by site differences which are related to variability in soils, aspect, moisture relations, slope, and other physical characteristics important to sagebrush (West 1983, Burke 1989, Burke et al. 1989, McLendon and Redente 1990, Young et al. 1990, Lane 1990). Differences between locations can also be caused by: 1) Small scale disturbances caused by insect and small mammal herbivory or pathogens (West 1983, Nelson and Sturges 1986, Nelson et al. 1990), 2) small scale stochastic events such as soil flooding (West 1983, Burke et al. 1989), and 3) episodic recruitment events (West et al. 1979, Reichenberger and Pyke 1990, Young et al. 1989, Young et al. 1990, Wagstaff and Welch 1991). Combinations of these factors will interact producing a continuum of responses in canopy coverage at the various locations. Mammoth had the highest amount of canopy coverage, suggesting this location was the most favorable for the support of sagebrush.

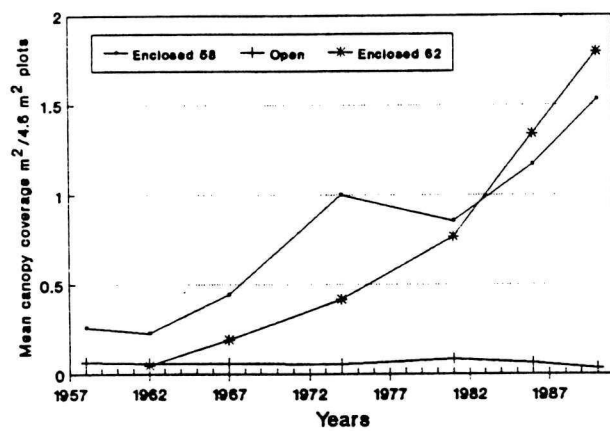
Some differences in canopy coverage are related to the belt's length which can include various microsites. Lane (1990), working with the soils at the same locations, found a high degree of small scale variability in soils due to the heterogenous glacial material or landslide deposits from which the soils are derived. This heterogeneity creates a patchwork of microsites each with a different potential for the support of sagebrush. Belts with a low sagebrush coverage probably represent locations where poor microsites for the support of sagebrush are predominate, while belts with higher coverage are dominate by better microsites.

Mammoth.--The Enclosed Belt at Mammoth differed in sagebrush canopy coverage, number of individuals, and canopy size distribution when compared to Enclosed Belts at other locations. At Mammoth there was a decrease in the number of individuals at the same time there was an increase in total canopy coverage. The arrangement of plant numbers contributing to the size distributions is different in that the larger canopy size classes had the most individuals. This results in few individuals being in the small classes, producing a reduction in the degree of inequality in the size distributions. The increase in canopy coverage, when combined with a decreasing number of individuals and size distribution inequality when found in other long-lived plants, such as trees, would be interpreted as self-thinning (Westoby 1984, Weiner and Thomas 1986, Knox et al. 1989). The process most often cited as causing self-thinning is intraspecific competition (Shugart 1984, Westoby 1984, Fowler 1986, Weiner and Thomas 1986, Huston and DeAngelis 1987, Knox et al. 1989). Intraspecific competition is a process that is often found when a population is at a density dependant state (Antonovics and Levin 1980, Westoby 1984, Fowler 1986, DeAngelis and Waterhouse 1987). No other belt had this pattern or had any other pattern associated with a state of density dependance. There is always the chance that other processes are responsible for certain patterns occurring in a population, and this is the danger of associating certain patterns with one process (Antonovics and Levin 1980, Phillips and MacMahon 1981, Fowler 1986, Huston and DeAngelis 1987, Ellis and Swift 1988, Cale et al. 1989, Collins and Glenn 1991).

Blacktail



Gardiner



Mammoth

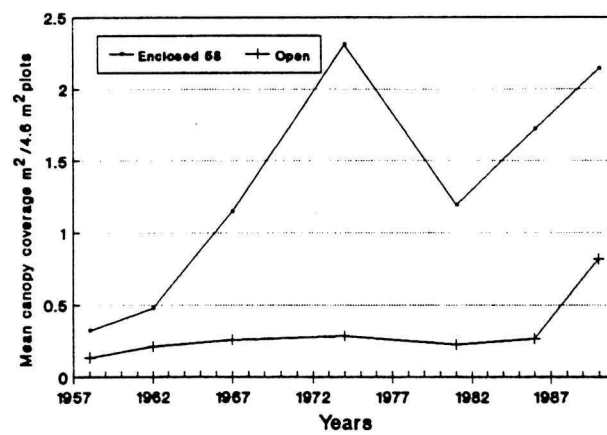


Fig. 2. Mean canopy coverage, m^2 , of the $4.6m^2$ plots for each year on each belt by location.

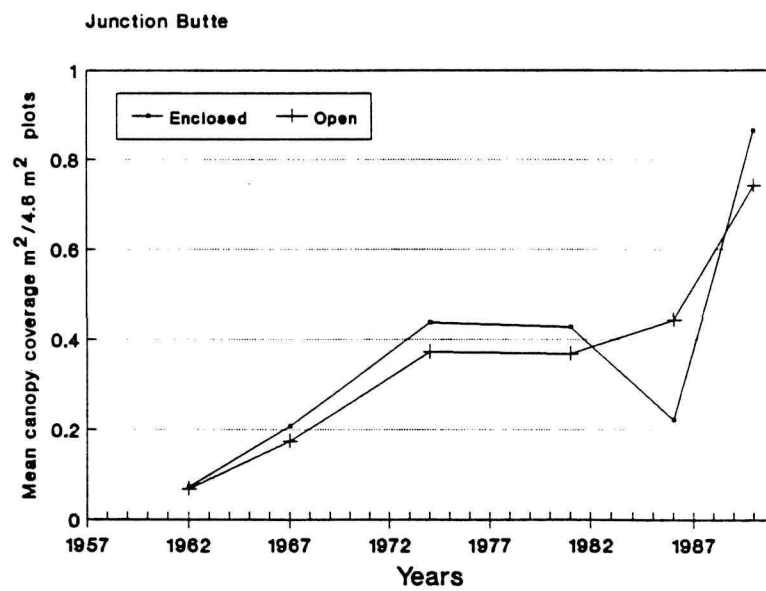
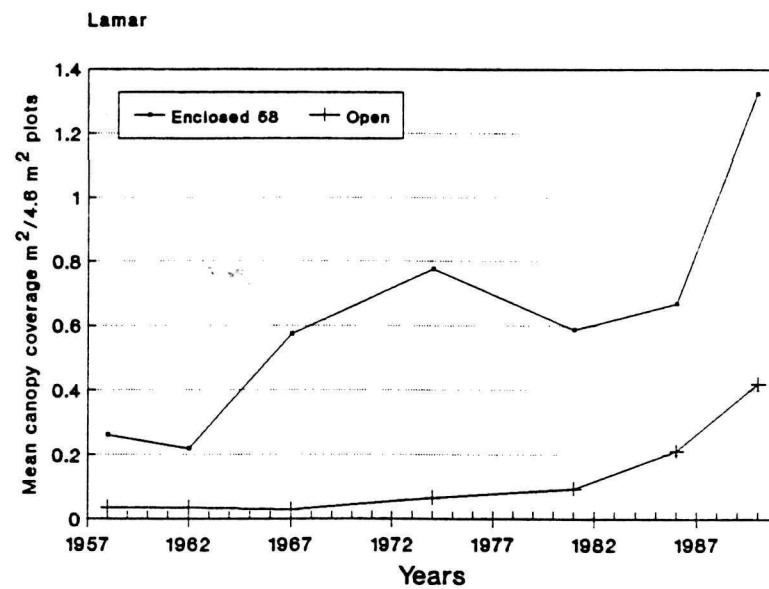


Fig. 2. Continued.

GARDINER ENCLOSED 1958

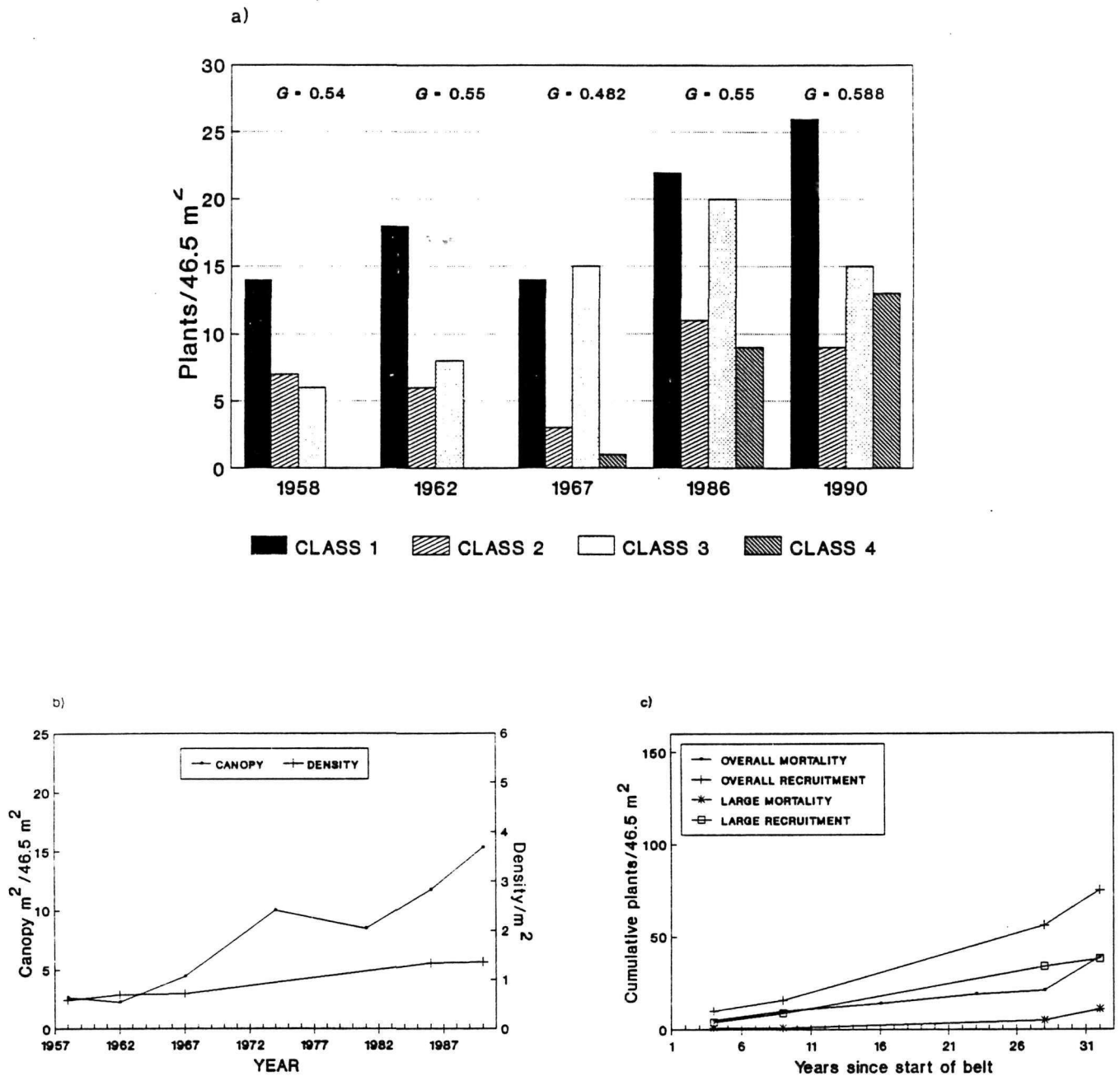


Fig. 3. Three belt demographic characteristics shown for each belt: 1) distribution of individual sagebrush over the four size classes per 46.5 m² for certain survey years with the Gini coefficient (*G*), 2) canopy coverage in m² per 46.5 m² for each belt survey year, along with density of sagebrush individuals per m², 3) cumulative mortality and recruitment since the start of each belt both for all plant sizes (overall) and for the large size category plants per 46.5 m².

GARDINER OPEN 1958

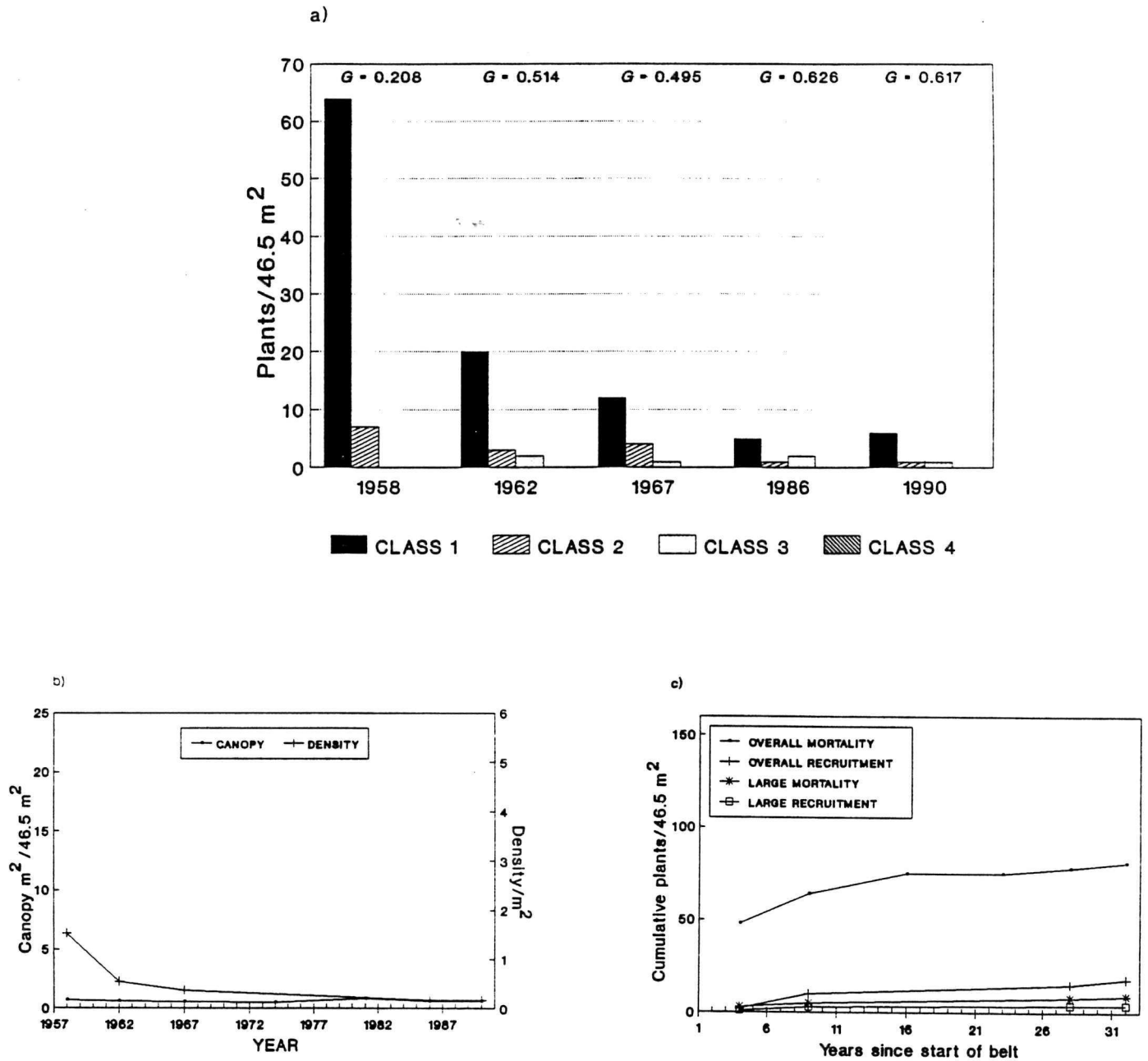


Fig. 3. Continued.

GARDINER ENCLOSED 1962

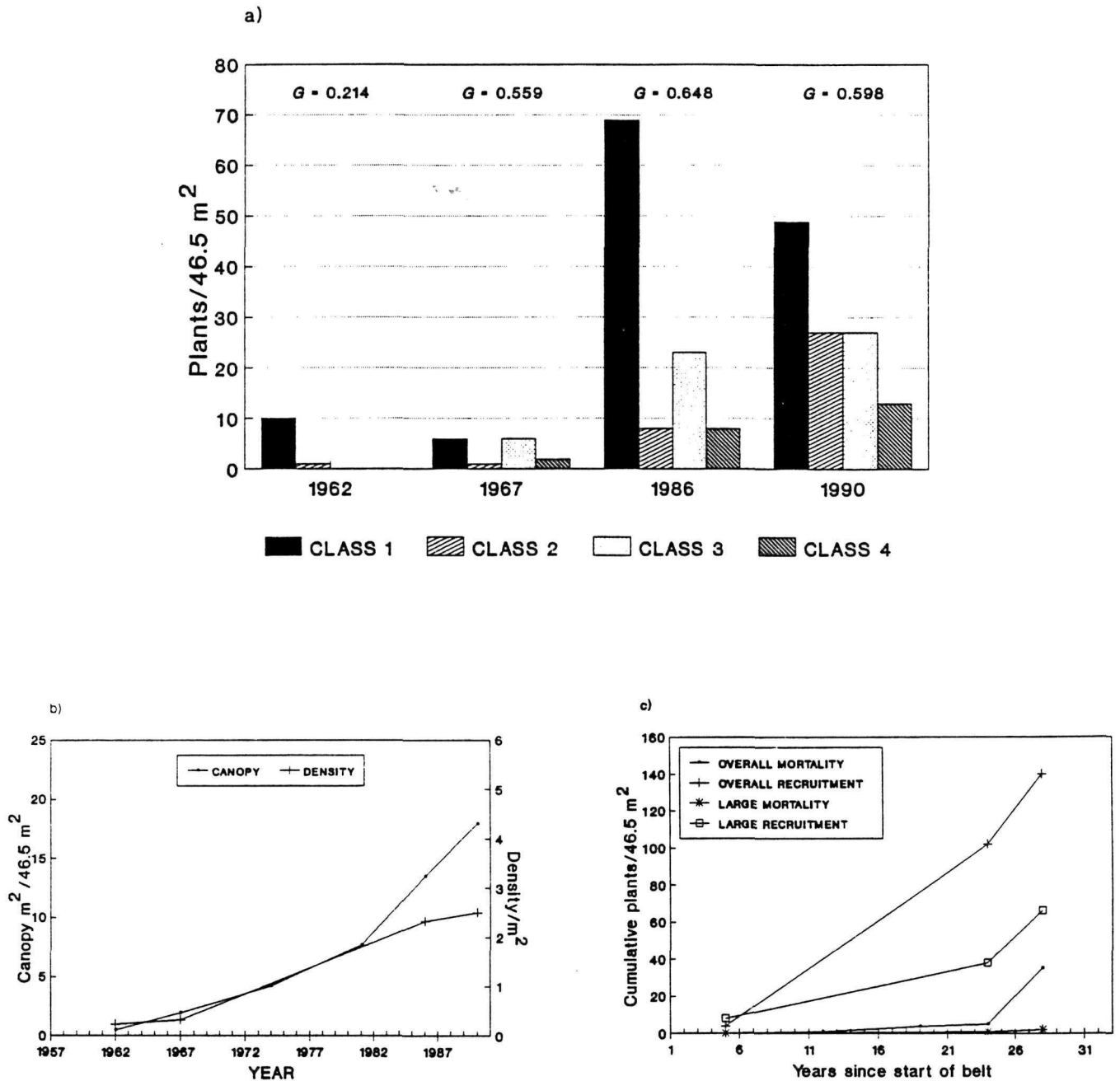


Fig. 3. Continued.

MAMMOTH ENCLOSED 1958

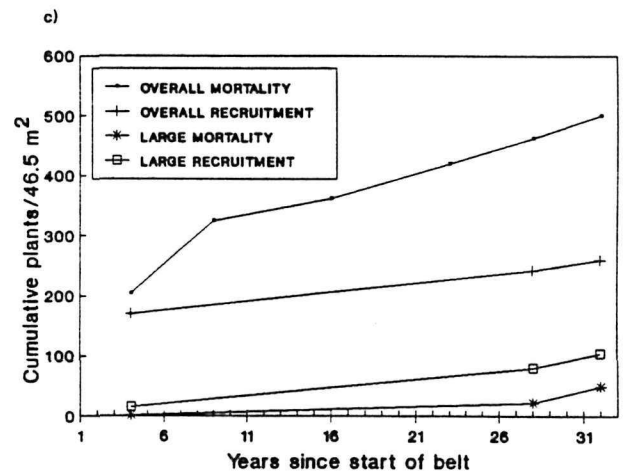
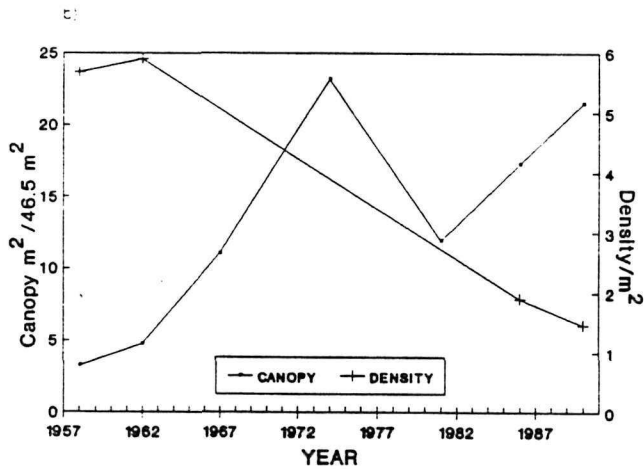
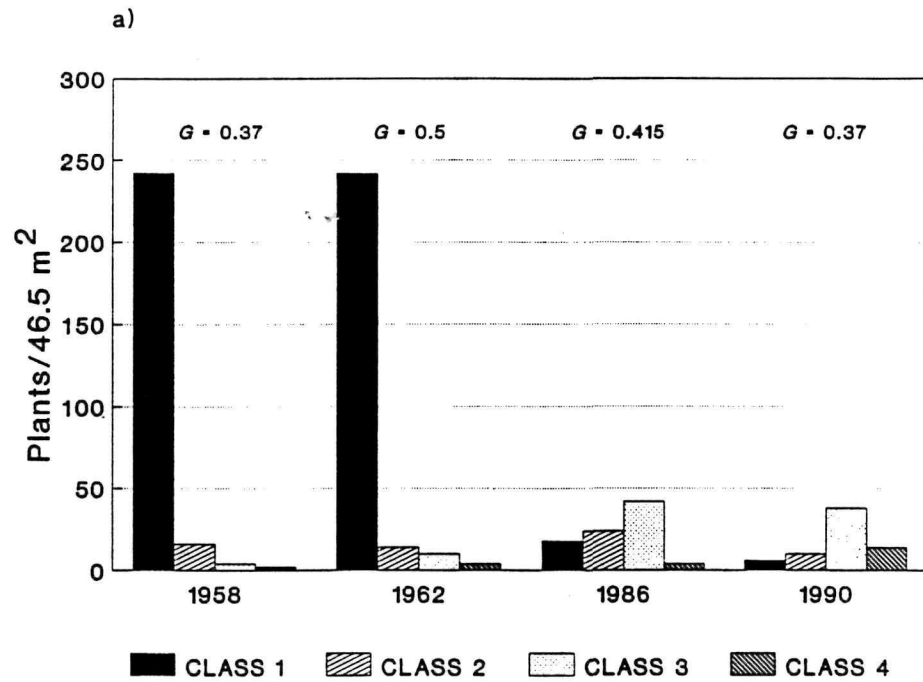


Fig. 3. Continued.

MAMMOTH OPEN 1958

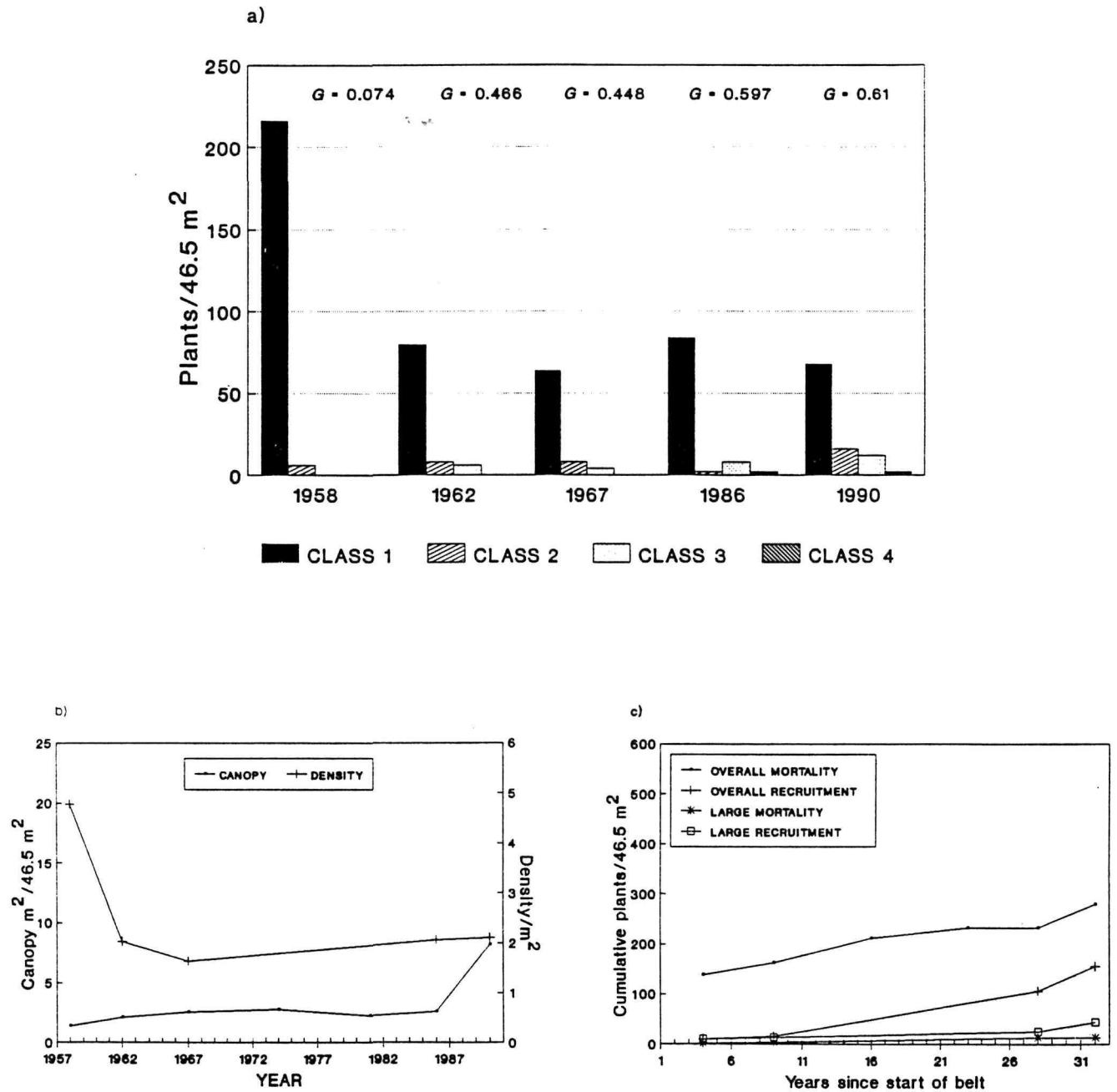


Fig. 3. Continued.

BLACKTAIL ENCLOSED 1958

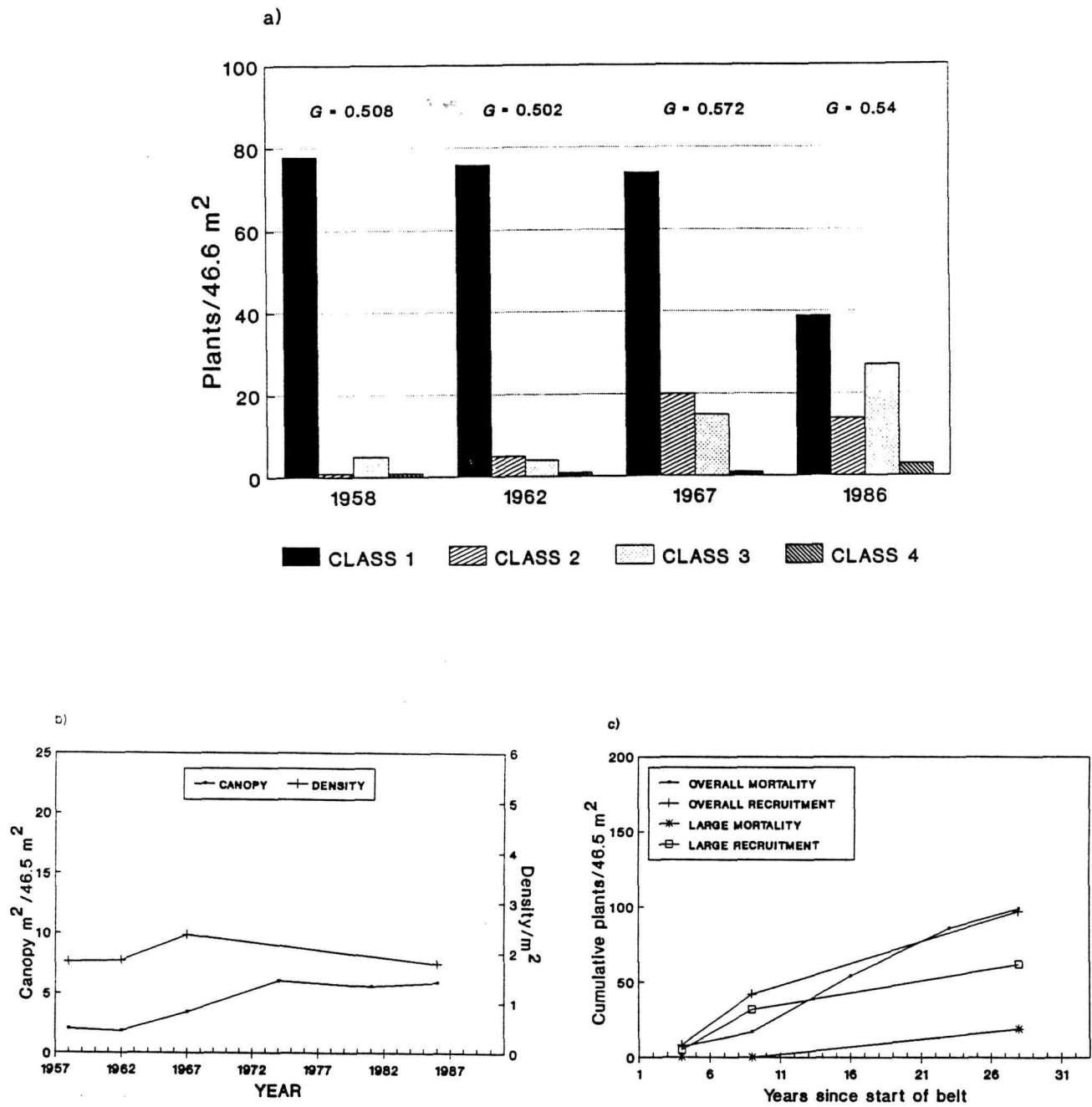


Fig. 3. Continued.

BLACKTAIL OPEN 1958

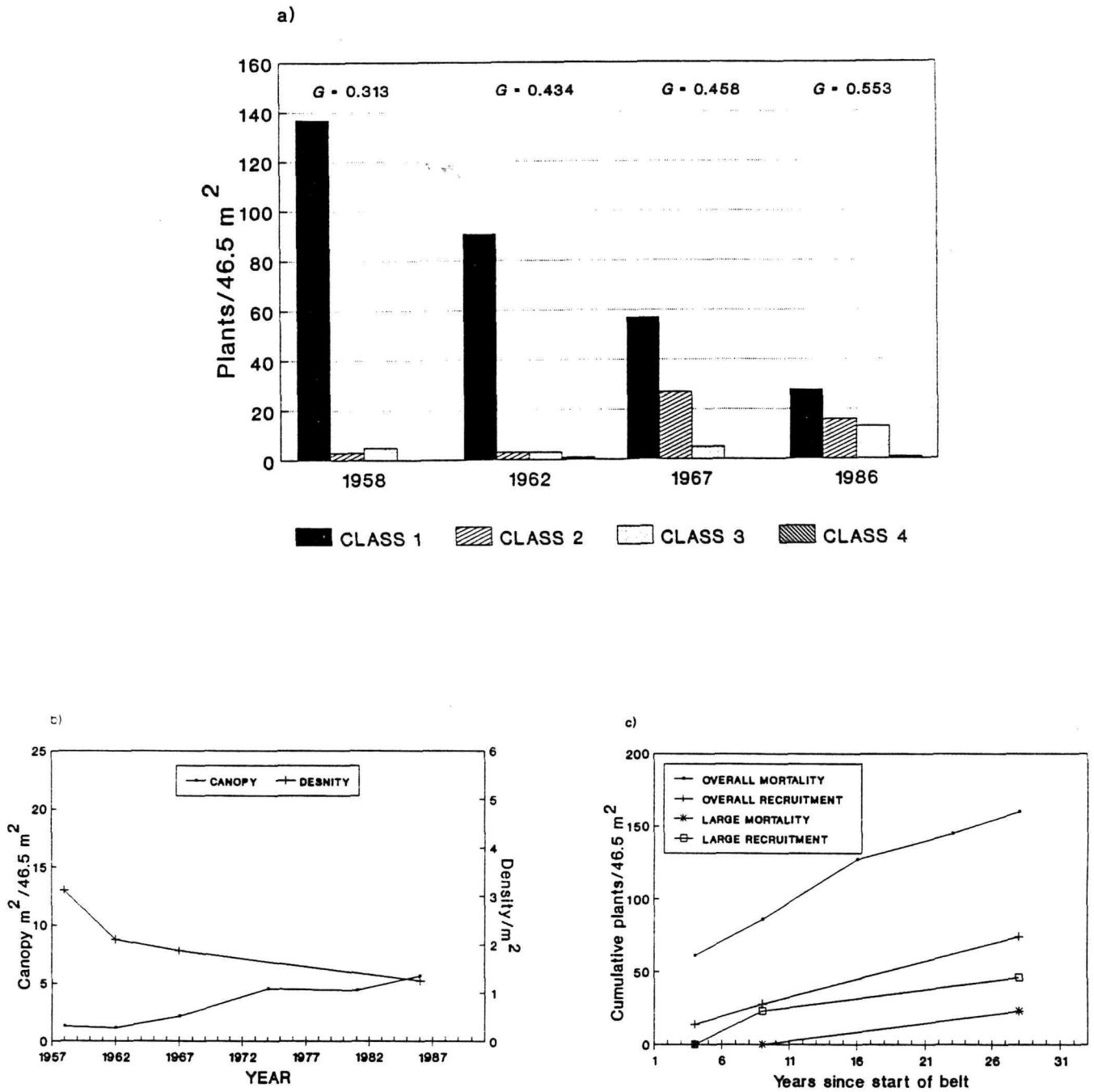


Fig. 3. Continued.

BLACKTAIL ENCLOSED 1962

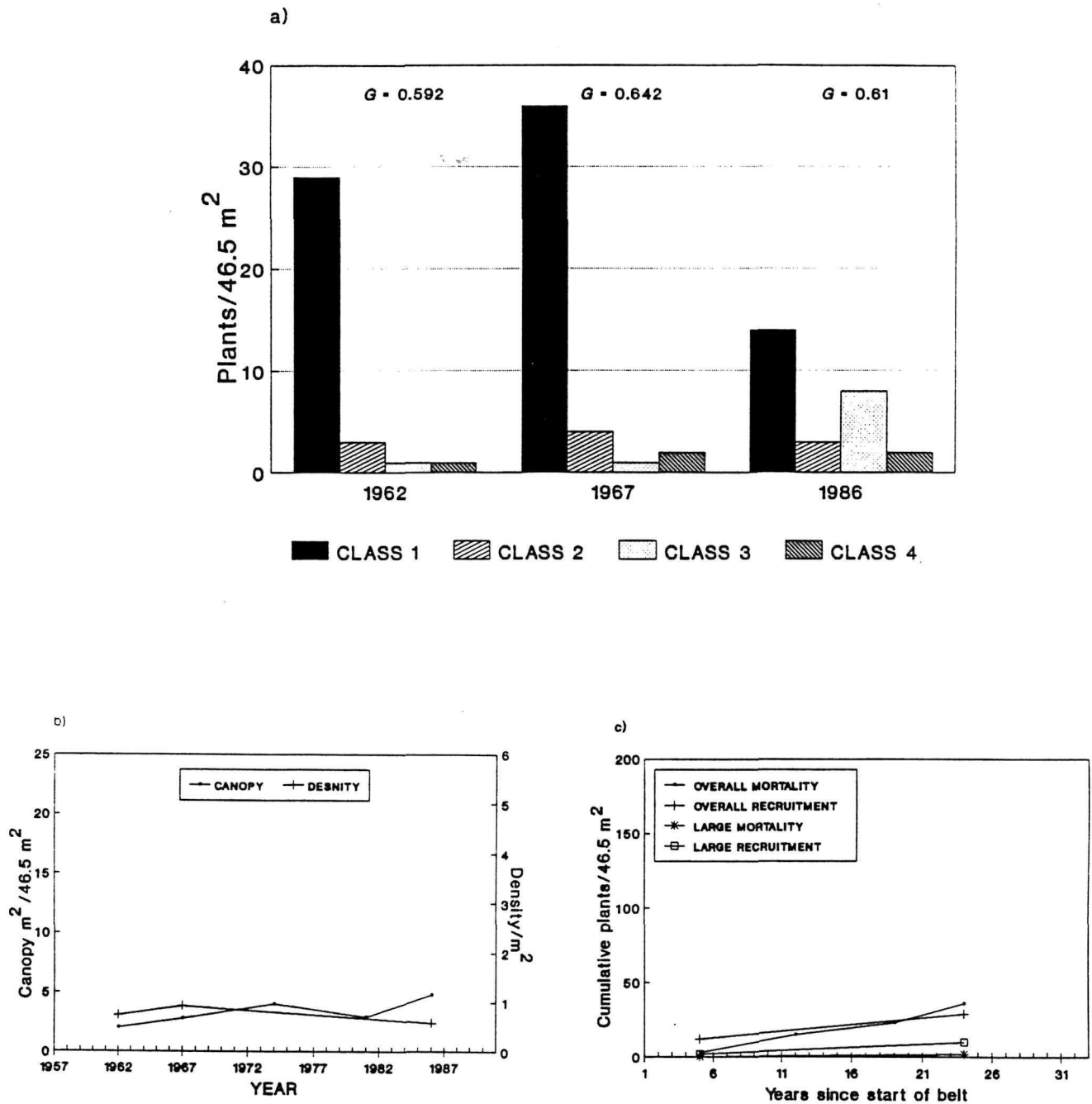


Fig. 3. Continued.

JUNCTION BUTTE ENCLOSED 1962

a)

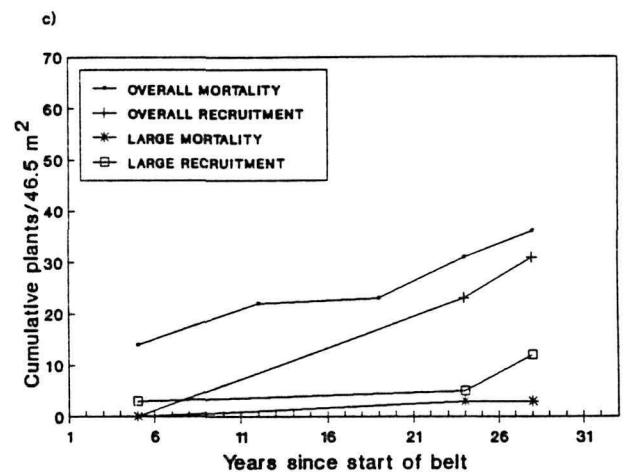
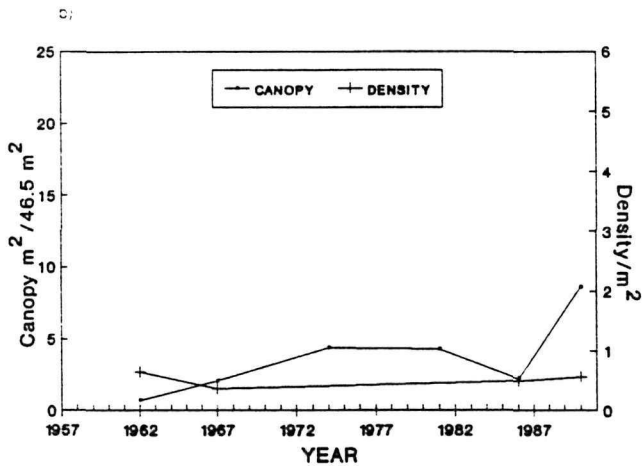
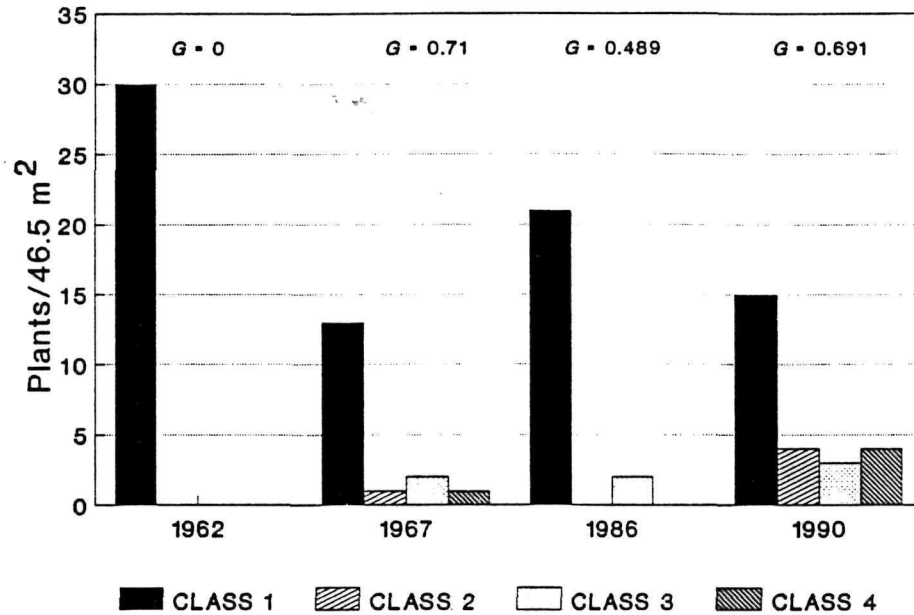


Fig. 3. Continued.

JUNCTION BUTTE OPEN 1962

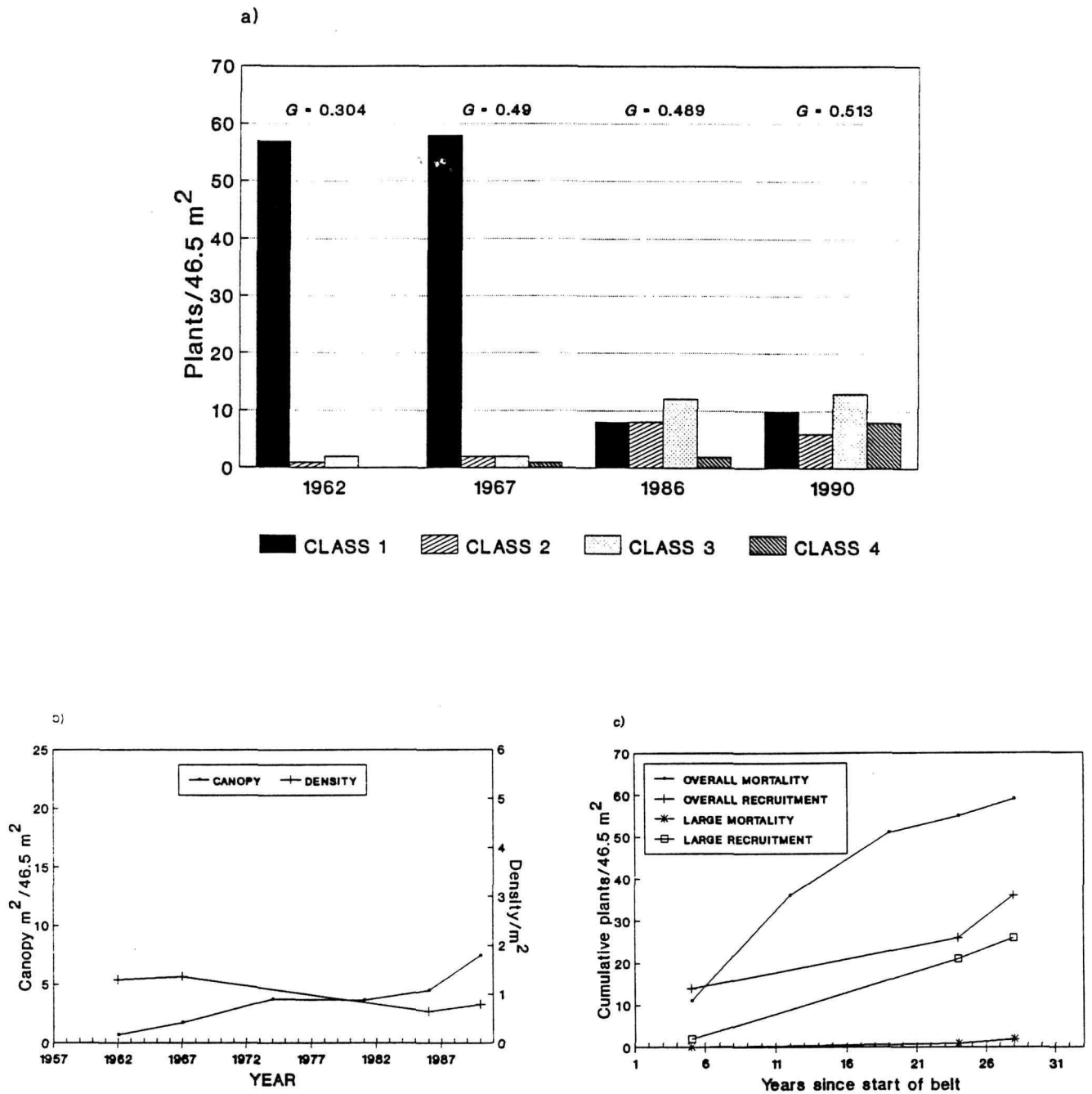


Fig. 3. Continued.

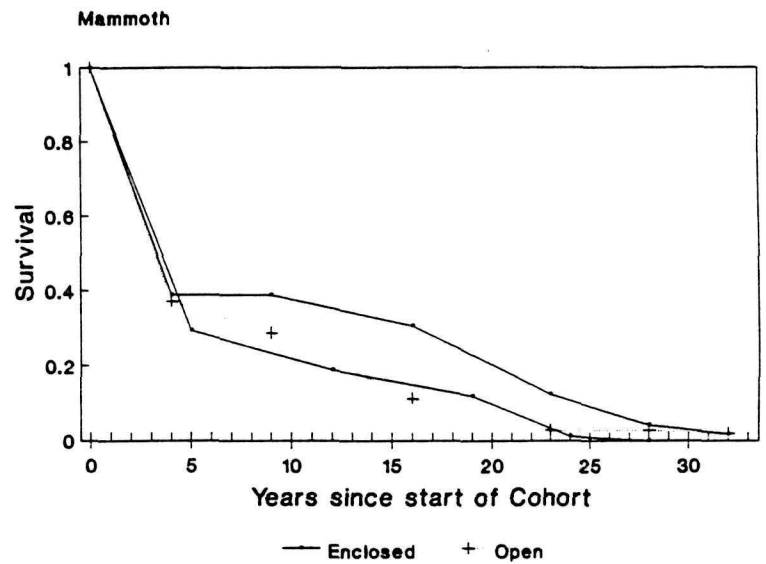
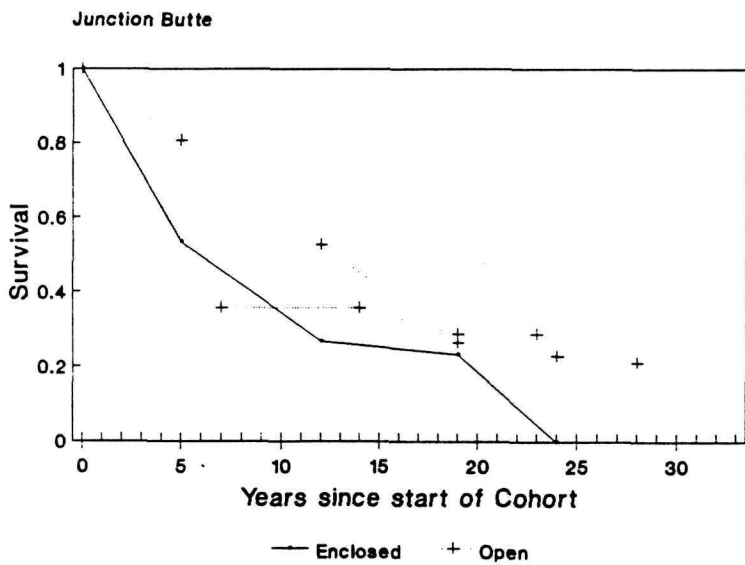
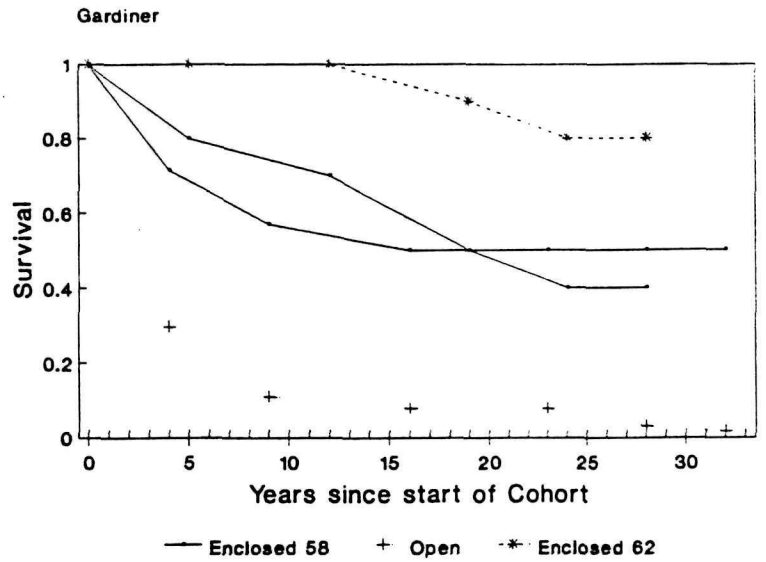
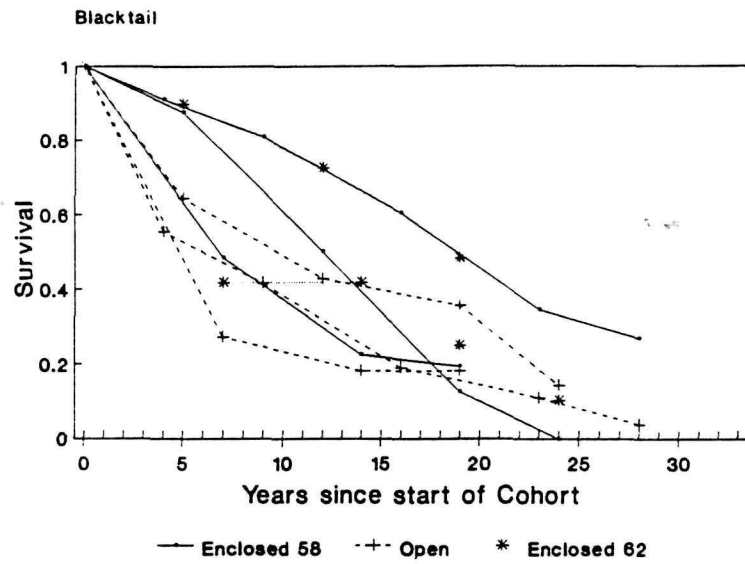


Fig. 4. Survivorship curves, percent of individuals surviving since the start of the cohort, by location, for the 1958, 1962, and 1967 cohort years which had at least 5 individuals at the start of the cohort.

Gardiner, Blacktail, Junction Butte.--The belts at Gardiner, Blacktail, and Junction Butte, do not exhibit the patterns found at Mammoth. These belts do not show any indication of self-thinning or density dependance (DeAngelis and Waterhouse 1987, Huston and DeAngelis 1987, Knox et al. 1989, McLendon and Redente 1990). The Enclosed Belts have increased canopy coverage, but there has not been a drop in numbers of individuals. In addition the inequality of the size distribution is still increasing. Sagebrush on these belts are growing with no sign of density-dependant regulation. The occurrence of interspecific competition on these belts is not unlikely, but its overall significance is masked by other equally important processes both deterministic (density dependant) and stochastic in nature. Given enough time and conditions conducive for development, the sagebrush at these sites should approach a situation similar to what is at Mammoth. Others have hypothesized that sagebrush, even after experiencing different disturbances, will eventually develop into populations similar in their demographic patterns given "long enough" (Anderson and Holte 1981, Hatton and West 1987, McLendon and Redente 1990). Until sufficient time has passed, these locations will not be similar in demographics to Mammoth, but will be in a process of developing into a state of density dependance. After 28-32 years, no pattern of self-thinning or density dependance has developed at these locations.

Survival and Recruitment.--A point in common to all belts is substantial variability in the patterns of recruitment and survival. Each belt's sagebrush survivorship curves exhibited a high degree of variability. Variability was also found in the rates of recruitment on the belts. The variability in recruitment has been noticed in other parts of North America and has been characterized as episodic (McArthur et al. 1988, Young 1988, Young et al. 1989, Young et al. 1990, Wagstaff and Welch 1991). This episodic recruitment along with the variability in adult survival is suggestive of populations controlled by events which have a stochastic nature. (DeAngelis and Waterhouse 1987, Huston and DeAngelis 1987, Fowler 1988, Westoby et al. 1989). This may explain why sagebrush populations at various locations do not exhibit the same canopy coverage or demographic characteristics. What pattern these stochastic events have on the northern range is unknown, but it is possible that certain sites may be predisposed to stochastic events or that stochastic events may happen independently (Huston and DeAngelis 1987).

Recruitment was evident on all the belts and recruitment into the large sagebrush canopy size category exceeded mortality on all belts except for the Open Belt at Gardiner. Even though recruitment was episodic, it is a common enough occurrence on the northern range even at Mammoth where the population was at a self-thinning stage. This common occurrence of recruitment is reflected in the turnover rates. The turnover rates of northern range sagebrush point to a life history where some individuals are long-lived (32+ years), but where the majority of plants come and go in a 25-year span. Such a fast turnover rate combined with the common occurrence of recruitment, show why sagebrush is such a dominate species on the northern range (West 1983). Sagebrush can dominate by being long-lived and can replace any mortality quickly.

The variety of conditions expressed in the sagebrush belts match those of "density vague" regulation (Strong 1984, 1986). Density vague regulation posits that at high population levels density dependance is the dominant process. At intermediate levels, density dependance is no longer dominate, but abiotic environmental fluctuations dominate. To prevent extinction, "floors" are present in the population that work to resist extinction. The mechanisms by which floors work has yet to be fully explored. Suggestions are that there are always sites where sagebrush can persist no matter what the abiotic conditions. Sagebrush can increase reproductive effort to overcome the increased mortality and stress, or immigration from outside the location can boost the population (DeAngelis and Waterhouse 1987).

Ungulate Use Effects

Because of the significant interaction between location and the Ungulate Use Treatment, it is not expected that the Open Belts had the same canopy coverage and demographic patterns as the Enclosed belts. The Open Belts at Gardiner and Mammoth have lower sagebrush canopy cover and differ in demographic

patterns in comparison to the enclosed. The Open Belts at Blacktail and Junction Butte appear to be the same as the enclosed.

Gardiner.--At the Gardiner location, the demographic pattern in the Open Belt was different from the Enclosed Belts. The Open Belt increased in the number of plants in the larger size classes, but the overall number of individual sagebrush decreased with no growth in the canopy coverage. Mortality in the larger category exceeded recruitment, a pattern not seen elsewhere. It is evident that the Open Belt is different than the Enclosed. The most obvious cause for the lower canopy coverage and differences in demographic patterns is due to browsing by ungulates. Ungulate browsing and physical damage from ungulate movements can potentially increase mortality of adult and young sagebrush, reduce recruitment, and reduce canopy coverage and size. Mule deer browsing on their winter range has been shown to be responsible for mortality and reduction of live crown of sagebrush (McArthur et al. 1988). Fall sheep browsing was shown to reduce longevity and survival of *Artemisia tripartita* (West et al. 1979). Clipping on sagebrush has been shown to result in mortality when done in the fall, winter, and spring with spring being the most sensitive time (Cook and Child 1971). Browsing on sagebrush on the northern range occurs from fall through spring (Barmore 1980, Houston 1982, Personius et al. 1987, Wambolt and McNeal 1987). A high proportion of sagebrush has been shown to be browsed at certain locations for various years on the northern range (Barmore 1980, Houston 1982, Personius et al. 1987).

Another possible explanation for the difference in Open to Enclosed Belts at the Gardiner location is that the subspecies found at Gardiner, Wyoming big sagebrush, is different than the subspecies, mountain big sagebrush, found on the other belts. Wyoming big sagebrush has been shown to be better adapted to arid conditions compared the other subspecies (Beetle and Johnson 1982, McArthur and Welch 1982, Barker and McCall 1983, Welch and McArthur 1986, Welch and Jacobson 1988). An adaptation of Wyoming big sagebrush is for the aboveground growth rate to be genetically controlled rather than allowed to develop according to the availability of resources (McArthur and Welch 1982, Welch and McArthur 1986, Welch and Jacobson 1988). This controlled growth rate has been proposed as an adaptation to arid conditions to prevent too much energy going to aboveground parts at the expense of below ground parts. Belowground biomass is more important for survival in arid environments because of the need for water absorption (Welch and Jacobson 1988, Booth et al. 1990). With such a control on growth, the compensation due to loss of photosynthetic material due to browsing may be restricted, making this subspecies less tolerant to browsing. Such a difference in subspecies could contribute to the differences in location to browsing. Another contributing factor to the difference in the Gardiner location could be that the area had in the past been altered because of man-controlled grazing by livestock (Houston 1982).

The high impact of browsing on the Gardiner Open belt sagebrush raises the possibility that not only will sagebrush continue as a minor part of the community, but may become locally extinct in this belt. The continued existence of sagebrush will be dependant on the proximity of a seed source and the availability of "safe sites" for the seeds to germinate and grow (Fowler 1988, Young 1988, Young et al. 1989, Young et al. 1990). Safe sites are microsites with special characteristics which promote the germination of seeds and the eventual survival of that seedling.

Mammoth.-- The demographic patterns in the Open Belt at Mammoth did show that there was growth in canopy coverage, development of sagebrush canopies into the larger size classes, and that recruitment was greater than mortality in the larger category. This kind of pattern in the Open Belt does mean that the sagebrush should continue as a major part of the community. What is different between the Open Belt and the Enclosed is that the Open Belt is not as strongly influenced by density dependant processes as compared to the Enclosed Belt. The Open Belt at Mammoth is a good example of competition being mediated by herbivory. Mechanisms for the lack of density- dependence dominance probably include ungulate use accelerating the mortality of older and younger sagebrush, preventing sagebrush from developing into larger canopy sizes, reducing the canopy coverage on the belt, and opening the belt up to recruitment. The

consequence of the Open Belt not being at the density dependence stage is that the sagebrush dynamics are not dominated by interspecific competition, but are dominated by the interaction of ungulates and sagebrush. With the interaction of the ungulates and sagebrush dominating the dynamics, the Open Belt should fluctuate somewhere below the level at which density dependence works, yet above a level where sagebrush no longer dominates the community. Exactly where the Open Belt will end up is dependant on the intensity of ungulate use and future changes in environmental factors.

Blacktail and Junction Butte.--The 2 locations that did not differ in demographic patterns from Open to Enclosed were Blacktail and Junction Butte. Both of these sites do have large numbers of ungulates foraging there during the winter, but the sagebrush appeared not to be affected according to the last survey. There has been browsing on sagebrush at these locations over time, as recorded by Barmore (1980) and Houston (1982), but browsing intensity was never measured. Because there is a lack of any information on the intensity of ungulate use on the sagebrush, it will be impossible to adequately explain the lack of an effect. It is possible that ungulates do not use the sagebrush at those sites, or the use is at levels which do not cause enough change in the sagebrush population in comparison to the Enclosed Belt. The fact that these 2 locations show no effects shows that ungulate use is neither uniform nor constant over the northern range. Another potential cause of the difference in location response to browsing is due to site differences. Sites which are stressful to sagebrush could produce indeterminate growth and fluctuations in the amount of growth per belt resulting in unstable growth. Sagebrush on good sites would produce different growth rates and more uniform growth. The effect of browsing on the stressful sites may not be as noticeable, because both Enclosed and Open Belts are unstable, and the action of browsing contributes to the instability.

Patch Considerations

The differences in sagebrush populations found in all of the Open Belts leads to the realization that each location has its own location-specific population dynamics. These localized populations can be considered subpopulations of the superpopulation of sagebrush on the northern range and are often referred to as patches or cells (DeAngelis and Waterhouse 1987). For the Open Belts at Junction Butte and Blacktail, the probabilities appear high that in the near future sagebrush will not decrease in importance, but will either stabilize or increase. The Open Belts at Mammoth and Gardiner will either not change or, more likely, decrease in importance, with the possibility that Gardiner sagebrush may become extinct.

All patch states collected together might produce what the overall picture of sagebrush condition is on the northern range. The condition of all patches on the northern range is unknown. Predictions about the overall condition of the sagebrush population on the northern range would require: 1) having a method to evaluate the population dynamics at each patch and, 2) a model on how these patches work together (Coughenour and Singer 1991). Such models of landscape ecosystem dynamics have been hypothesized and some success has been made in predicting the long-term and region-wide dynamics of forest ecosystems (Shugart 1984, DeAngelis and Waterhouse 1987, Harrison and Shugart 1990). Developing a landscape model based on the transient dynamics of sagebrush patches and verifying that model with data from northern range would go a long way toward understanding and predicting sagebrush dynamics on the northern range (Coughenour and Singer 1991).

Management Implications

The effects of ungulate use reducing canopy coverage may translate into less sagebrush forage produced. Sagebrush is an important forage item for wintering ungulates because it is a good source of nitrogen and energy during a time of year when the other forages are low in nitrogen and energy (YNP, unpubl. data) (Hobbs et al. 1982, Hobbs and Swift 1985, Striby et al. 1987, Hobbs 1989). The reduction in forage availability of sagebrush means that the opportunity for ungulates to forage on a high protein, high energy source is reduced. The reduction in opportunity may or may not result in lower ungulate survival. If other forages are present that can be substituted for the sagebrush without any reduction in protein or energy intake, then the effects of lower sagebrush availability may not result in lower ungulate survival. However, if

no other substitutable forage is present, then the lower protein and energy intake for the ungulate may result in lower ungulate survival.

Recruitment and regeneration of sagebrush is not dependant on disturbance. There has been continued recruitment over time at the each of the locations. The sagebrush in the larger size classes (seed producing) are composed of individuals which originate from various cohorts and are at various ages. This all-aged or multi-cohort age structure promotes continued persistence of sage especially at those locations where sagebrush is not affected by browsing (West et al. 1979). It is possible that a set of conditions will develop in the future that will prevent regeneration, but the last 20 to 30 years have resulted in no periods without recruitment. Given that conditions do not change too swiftly, the continued persistence of sage is assured. The persistence of sage does not mean that sagebrush populations will not continue to be affected by ungulate use. Given that ungulate population levels will remain at or close to the current levels, there is the potential for ungulate use effects to be compounded.

The fact that sagebrush works at a patch level in the park means that more complicated methods such as landscape modeling are needed to judge the condition of sagebrush over the landscape. Looking at only a few selected patches could result in conclusions of effect, or no effect, when the majority of patches are reacting otherwise. Based on the fact that sagebrush has been a constant part of the Yellowstone ecosystem since the last glaciation (Engstrom et al. 1991) the sudden loss of sagebrush is not anticipated, but fluctuations at a local scale and on a landscape scale may take place (Coughenour and Singer 1991).

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