

Vegetation Responses of an Old-Field Ecosystem to Single and Repeated Sulfur Dioxide Disturbances

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Abstract. Quadrats of a first-year old field on the New Jersey Piedmont were treated with single 1 ppm SO₂ disturbances for 4-hour periods. Clip sampling revealed up to 47% reduction in living biomass immediately following single disturbances early in the summer, and a progressive decrease in damage when the disturbance occurred during the later months of the growing season. Late season grasses (*Setaria* spp., *Digitaria* spp., and *Panicum* spp.) were more resistant than the forbs (*Raphanus raphanistrum*, *Ambrosia artemisiifolia*, *Convolvulus sepium*, and *Solanum carolinense*), and all species, except *Convolvulus*, became more resistant to SO₂ disturbance subsequent to flowering. As a result of posttreatment recovery, total end-of-season standing crop of herbage, treated previously in mid-July and early August, was not significantly different from undisturbed control vegetation.

The recovery of vegetation cover following single and repeated disturbances occurred as a result of: (1) increased growth rates of virtually all species and (2) a restructuring of the species composition of the plant community by more than doubling late season grass cover in some SO₂-treated vegetation. Repeated disturbance produced greater total damage, increased species and total herbage growth rates, changed species composition more, and produced a greater excess of living tissue above control levels at the end of the growing season in comparison with single SO₂ treatments. The response varied with the length of the interval between treatments. A 3-day separation resulted in a greater decrease in tissue from control levels and higher subsequent growth rates. In contrast, disturbances separated by a 15-day interval produced greater total tissue damage, because the second disturbance killed more regrowth tissue and resulted in more extensive changes in the species composition.

A single disturbance produced a 17% reduction in the amount of photosynthetic surface area totaled over each day of the postinitial treatment growing season. In the case of repeated disturbances, the reduction was 24% if the interval between SO₂ exposures was 3 days, and 32% if there was a 15-day separation between disturbances. Therefore, the overall community impact of more widely spaced SO₂ treatments of the same intensity was greater than that of the same disturbances occurring over a brief interval.

Introduction

The recurrence of disturbance is now recognized as an inherent property of ecosystem structure and function. The effects of natural disturbances, such as fire, windstorm, ice storm, extreme temperatures, lava flows, and flood or drought, have been reviewed by White (1979). Anthropogenic sources of disturbance, such as pollution, are also significant and produce effects similar to those attributed to natural impacts (Woodwell 1970). Levin (1976) indicates that there is a "virtual continuum between the types of perturbations which are 'natural' and those which are man-made." The study of responses of ecosystem components to disturbance has been central to ecology from the earliest investigation of plant succession. The literature, as reviewed by Golley (1977), indicates that virtually every parameter changes during the course of ecosystem development.

Grime (1974) has made a useful differentiation between stress, which prevents the development of a large vegetative standing crop by restricting primary production, and disturbance, which reduces biomass by causing physical damage. The success of species within plant communities is a result of their inherent competitive ability and the presence of strategies to cope with stress and disturbance.

One method of assessing the impact of disturbance on an ecosystem is to manipulate a community experimentally and, subsequently, monitor various responses. Cocking (1973) used this procedure to apply an experimental disturbance to a first-year old-field ecosystem. This was accomplished through fumigation with a short duration (4 hour), acute (1 ppm) SO₂ exposure; part of that study is reported here.

Sulfur dioxide has long been recognized as an atmospheric pollutant which causes injury to plants and disturbance to the ecosystem. The physiological action and effects of this toxicant are reviewed in Stern (1978) and Mudd and Kozlowski (1975). Species-specific variation in susceptibility of herbaceous plants to SO₂ is well-documented (Treshow 1970), and the age of specific tissues has also been shown to be extremely important in determining relative susceptibilities (Setterstrom and Zimmerman 1939). Therefore, since the species present in an old-field ecosystem are not synchronous in their phenology (Malone 1968), signifi-

cant differences in susceptibility of the plant community to SO₂ should be expected at different times during the growing season.

The first objective of this study was to determine whether, in a naturally occurring plant community, there was a temporal and species-dependent pattern of response to sulfur dioxide disturbance. The impact of repeated disturbance is not necessarily additive. Three alternative hypotheses were examined concerning the susceptibility of a previously disturbed ecosystem: (1) the system would become more susceptible to a second disturbance, possibly because it had been weakened by the first episode, (2) the system would be more resistant to a second disturbance, either as a result of a loss of sensitive individuals or through reduction in sensitive tissues, and (3) a preconditioning disturbance would have no observable effect on the response to a second disturbance. The time interval between disturbances could also affect the impact of a second fumigation, and, therefore, the second objective of this project was to determine which of the three hypotheses was best supported in the case of two disturbances applied over a short (3-day) or long (half-month) interval, in comparison with vegetation which was disturbed only a single time.

A third objective was the description of the mechanism of recovery following the disturbance, which could involve increased growth rates of damaged individuals, changes in species composition, or a combination of both mechanisms. The fourth objective was to develop an index related to plant community function which would quantitatively estimate the total impact of the disturbance.

Study Area

Experimental work was carried out at the Hutcheson Memorial Forest of Rutgers University, situated 2 km east of East Millstone (40°30'N, 74°34'W) on the Piedmont of New Jersey. The soil is a well-drained loam largely developed from the Triassic red shale of the Brunswick formation with a poorly developed profile (Ugolini 1964). The 2-ha area utilized, fields D6 and D7 of the permanently established grid system, had most recently been plowed, disked, and allowed to go fallow in the spring of 1970. Field topography was relatively even with a 3-4% slope dropping to the northwest. All experimental blocking was oriented along this contour. In 1971, the field was plowed on May 4 and given a final disking on May 20. In 1972, the same area was plowed on April 27 and disked on May 7. There was a buffer zone of herbaceous old-field vegetation extending at least 75 m on all sides of the study area. Further information on the plants and environment of the surrounding fields is available in Bard (1952), Small (1973), and Allen and Forman (1976).

Environmental data were obtained during the experimental periods using a Belfort recording pyrliometer

and sheltered Friez hygromographs, which were placed at soil level within the herb layer. Temperature maxima and minima and rainfall were recorded daily at the Hutcheson Memorial Forest climatological station 250 m distant. Ambient pollution levels were not monitored regularly. However, both treatment and control vegetation were exposed to the same conditions except during experimental fumigations.

Methods

Layout of the Experimental Plots

Experimental grids were established each year within the 2-ha disked field. The grids were always at least 10 m from the edge of the plowed area. In 1971, the grid was eleven plots wide and eight plots long with the plot dimensions being 7 x 10 m. In 1972, the grid was two plots wide and eight long with the dimensions being 15 x 10 m. A 1-m-wide mowed trail was maintained along the boundary lines between plots for the duration of the growing season. Some of the plots within the 1971 grid were excluded prior to the start of the experimental treatments due to the presence of a plow furrow which bisected the grid, and also due to a depression in one corner of the field. After the exclusion, there remained a total of 72 potential plots, from which 25 were randomly selected for use. In 1972, all of the plots within the grid were suitable for experimental use. The specific locations of individual plots within each year's grid are reported elsewhere (Cocking 1973). The grid was blocked into three sections in 1971 and two sections in 1972 for the purpose of designed statistical testing by the analysis of variance (ANOVA). The experimental design for treatment application and the sampling techniques were different in the two years and will be discussed separately.

Methods of Applying Disturbance

Sulfur dioxide fumigation was accomplished through the use of a pair of wood-frame, translucent, polyethylene-covered 3.5 x 3.0 m chambers having a maximum height at the roof peak of 2.0 m. The chambers were constructed in modular, flat sections that could be assembled within 1 hour by two persons without walking on the herbage to be treated. Unfiltered ambient air was circulated through the chambers by a Dayton shaded pole blower, rated at 980 cfm against standard atmospheric pressure, which was mounted in a baffled mixing box. The volume of the chamber was 17.3 m³ (611.8 ft³) and, therefore, the fan had the capability of turning over the air within a chamber in approximately 3 min. Vegetation movement within a chamber due to the fan appeared similar to that outside of the chamber with a wind speed of 5-10 km hr⁻¹. Sulfur dioxide was supplied from a Matheson gas cylinder of anhydrous grade (99.98% pure SO₂) gas. The flow rate was regulated by a 21RS4 Whitey valve, and the gas was carried through Tygon tubing

to the mixing box. The concentration of gas within the treatment chamber was monitored with a Scientific Industries Model 67 SO₂ analyzer connected to a Teflon air-sampling tube. The concentration was manually regulated during the fumigations within a range of approximately 0.8 to 1.2 ppm.

The standard treatment was a single exposure period of 4 hours that commenced between 8 and 9 a.m. daylight saving time. Soil moisture within the chambers at the time of treatment was determined by collecting six 2-5 cm subsurface samples with a trowel, and weighing the samples before and after drying at 105°C for 24-96 hours. The temperature and relative humidity 6 cm above soil level within the chambers were monitored with Friez hygrometers.

Conditions during SO₂ Fumigation

Mean values for temperature, soil moisture, and VPD (vapor pressure deficit, calculated from relative humidity and temperature readings during the fumigation periods) are plotted for each week during the 1971 growing season (Fig. 1). There was considerable variability in the conditions, both within a given fumigation period, since the ambient temperatures rose during the morning hours, and among treatment days. The most extreme hourly temperature average recorded during any of the 1971 fumigations was 17°C and 43°C. However, the extreme hourly averages were generally more moderate, with maxima greater than 38°C or minima less than 22°C occurring during only 16% of the fumigations. Relative humidities ranged from a maximum of 100% to a minimum of 30%. During 90% of the fumigations, the relative humidity was at least 75% when the treatment period commenced, and

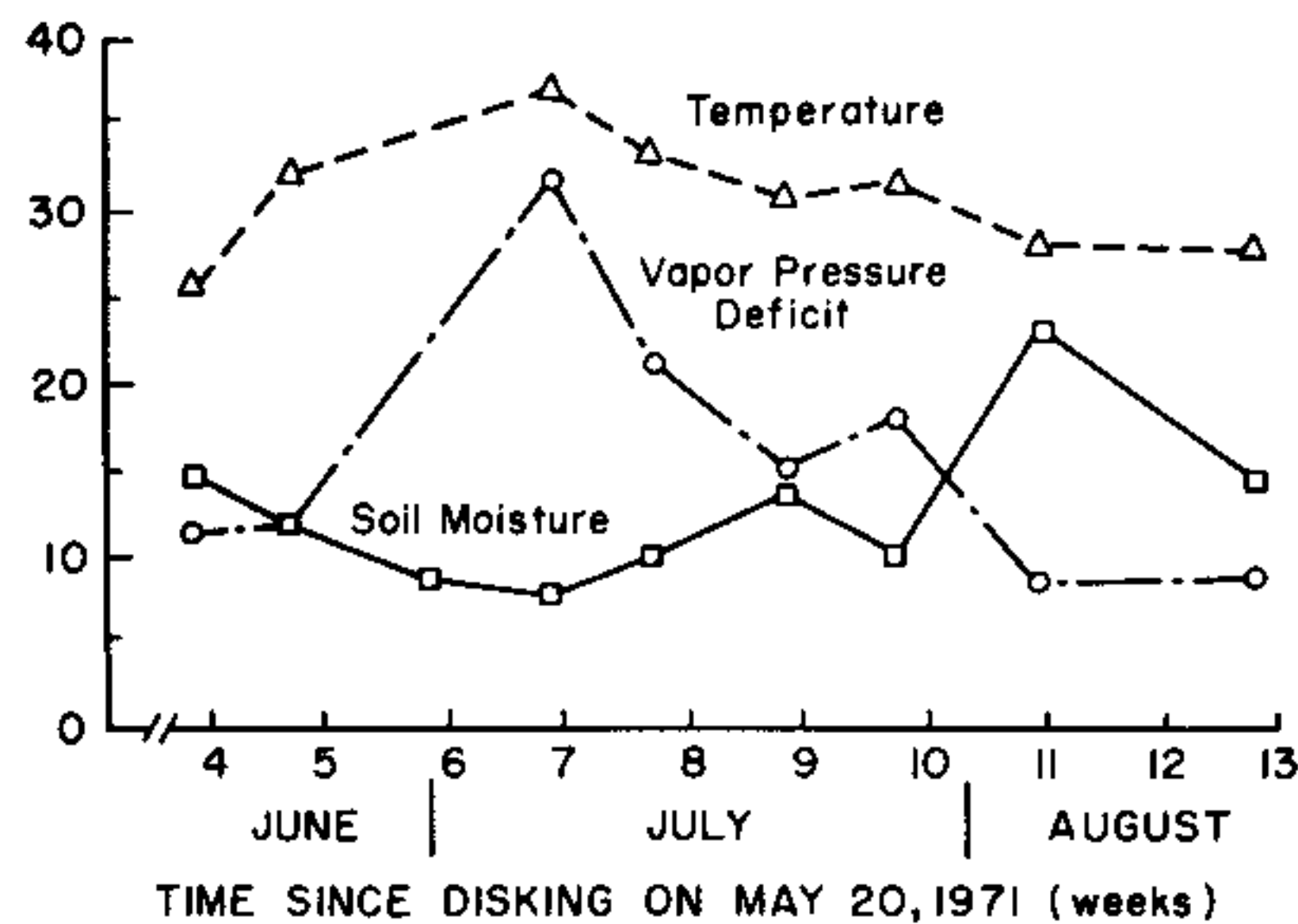


Fig. 1. Average 1971 environmental conditions within the fumigation chambers during the 4-hour-treatment applications. Vertical axis: VPD = mean chamber vapor pressure deficit (mm Hg); Temperature = mean chamber temperature (°C); Soil Moisture (%).

in 74% of the cases it never dropped below 50% during the exposure period. The conditions within the chambers during fumigation periods in 1972 were within the range of those recorded in 1971.

Multiple linear regression analysis of the damage due to SO₂ fumigation as a function of the mean temperature, soil moisture, and VPD conditions during the fumigation period failed to show a significant correlation of damage with any parameter. This was probably due to the limited number of cases rather than to a lack of environmental effects.

Experimental Design—1971

In 1971, a two-phase experiment was designed to assess the extent of damage caused to the plant community by single exposures to acute SO₂ stress. The data were all subjected to appropriate factorial analyses of variance. The initial part of the experiment was carried out in mid-June during the fourth week following disking. On four successive days, the two chambers were erected next to each other within a randomly chosen 7 x 10 m plot. One chamber was used to expose vegetation to the standard fumigation of approximately 1 ppm SO₂ for 4 hours in the morning. The other chamber circulated only ambient air and was used as a control. The 3.5 x 3.0 m area of vegetation covered by a chamber will be referred to as a quadrat. The chambers were removed from the quadrats by midday and the vegetation was left to grow for 1 week. Six to 8 days after fumigation, vegetation from two rectangular 0.5m² randomly selected sample areas was clipped at ground level from each of the eight quadrats and separated by species, using the techniques described in the next section.

In the second part of the experiment, pairs of quadrats were fumigated, in the same manner described above, within one plot chosen at random from each of the three statistical blocks during the 5th, 7th, 8th, 9th, 10th, 11th, and 13th weeks following disking. The last fumigations were carried out near the end of August. The quadrats were clip-sampled on the 7th day after the midpoint of the fumigations of the previous week. Finally, the six pairs of quadrats which received treatments during weeks 8 and 11 following disking were also clip-sampled in September during the 16th week after disking.

Regression analysis with the statistical package on a Hewlett-Packard 980 desk calculator was used to determine the best fit equations for the standing crop of control vegetation, and herbage treated the previous week, over the course of the growing season.

Clip-Sampling Technique—1971

Individual plants within a rectangular 0.5 x 1.0 m randomly selected clip-sample area were cut at ground level, and all of the standing living and dead tissue, plus the current season litter, was placed in a polyethylene bag. Two such random samples were obtained from a quadrat whenever it was examined. The tissue was

separated manually into living and dead tissues, and, taxonomically, as two grass components, *Agropyron repens* (quack grass) and the miscellaneous grasses which included species of *Setaria* (foxtail grass), *Digitaria* (crabgrass), and *Panicum* (panic grass). Four forb species, *Raphanus raphanistrum* (wild radish), *Ambrosia artemisiifolia* (common ragweed), *Convolvulus sepium* (hedge-bindweed), and *Solanum carolinense* (horse nettle) were also separated, in addition to a small number of miscellaneous forbs. Identifications were made according to Gleason and Cronquist (1963). Green tissues were considered to be alive, as were stems bearing green tissues. Since this was a first-year old field, all nongreen tissues were considered dead, and leaves or plants having both types of tissues were physically torn and the parts apportioned to the appropriate categories. Most of the separations were accomplished within a 48-hour period after clipping, and the tissues were placed in cold storage during this period at 5°C to reduce respiration and eliminate decomposition. When this was not possible, the herbage was frozen at -18°C until it was sorted. All separated tissues were then oven-dried at 105°C for 24-96 hours and weighed to determine the standing crop within a 0.5m² sample area.

Nondestructive Point Sampling Technique—1972

In 1972, the objective of the experimentation was to follow the recovery pattern of disturbed plant communities and compare their composition with undisturbed control vegetation. Therefore, a nondestructive technique for sampling plant cover was utilized. A point-frame apparatus was constructed consisting of a 1.0 x 0.5 m table, 1 m high, with left and right sets of ten randomly located holes which were drilled at angles approximately 20° to the perpendicular (Cocking 1973). The holes were lined with aluminum tubing to allow a pointed steel rod to slide freely in a fixed trajectory. The data for a single point were obtained by passing the rod through the aluminum tube and recording all plant tissue between the table and ground surface that was hit by the 1-mm-diameter tip. Each plant hit was classified into the groupings used in 1971 and according to whether the tissues were living or dead.

This device, developed specifically for this study, was used to obtain data in the following manner: The rod was passed through each of the twenty holes in the table each time the frame was placed in the vegetation. The data from the ten points on the left and the ten points on the right were summed separately, resulting in two estimates of the "number of hits for ten passages of the rod through vegetation" for each species. This was used as a relative cover index, and the frame was placed within the vegetation six times when a quadrat was sampled. Therefore, twelve measures of this index were obtained from an initial total of 120 trajectories and averaged to produce the "relative cover index." The units of the three-dimensional cover index used in

1972, therefore, are arbitrary (number of hits in ten linear trajectories through the vegetation) and not directly convertible to biomass of the standing crop. This statistic is a quantitative measure of how the space between the soil surface and the top of the vegetation is filled, and is, therefore, a proportional measure of standing crop. Differences in tissue density, biases due to more frequent hits of highly dissected leaves, and geometric pattern within the vegetation are undoubtedly present, as in all point frame techniques (Greig-Smith 1964).

Experimental Design—1972

In 1972, the effect of repeated SO₂ fumigation on herbage, and the recovery patterns subsequent to disturbance, were examined using the nondestructive sampling technique described in the previous section. In 1971, one chamber had been used as a control circulating ambient air, and the other administered the SO₂ fumigation on each day of treatment. The short 4-hour duration of the fumigation period was not sufficient to cause wilting in the control chamber, and the temperature and relative humidity conditions were always within the range of those outside the chamber. There was no evidence to indicate any effect of the ambient air circulation on the vegetation. Therefore, in 1972, both chambers were used for fumigation since mechanical limitations prevented the use of more than two chambers. Pretreatment sampling 24-48 hours prior to treatment was used as a control for comparison with the effects 24-72 hours subsequent to treatment within both chambers. In addition to these pretreatment samples, two plots which were never disturbed experimentally were selected at random, and two quadrats contained within them were sampled at three additional times during the growing season—the 12th, 14th, and 18th weeks subsequent to disking—for additional estimates of the cover of untreated control vegetation. The "relative cover index" for all treatment or control vegetation estimates is, therefore, based on six placements of the "point-frame device" within each of two quadrats of a plot. Since a plot for each control or treatment regimen was included within each of the 1972 statistical blocks, each estimate of plant cover is an average of 480 "passes of the steel rod through the vegetation type."

Three treatment regimes were used in 1972. All treatments involved an SO₂ fumigation in the 9th or 10th week after disking during the first 2 weeks of July. The four quadrats receiving this single exposure are referred to as T1. A second set of four quadrats, T2, received a repeat exposure 3 days after the initial treatment; a third set of quadrats, T3, received the repeat exposure one-half month later during the 12th week following disking. This involved an intricate sequence of fumigations since only the two quadrats on a single plot could be fumigated each day. The specifics of this procedure are outlined elsewhere (Cocking 1973). The

quadrats receiving all three treatment regimes were also sampled in July and August during the 12th, 14th, and 18th weeks subsequent to disking, for comparison with the untreated control vegetation cover.

Results

Growth of Untreated Vegetation

The pattern of accumulation of living plant tissue within the experimental fields and the distribution of rainfall are compared in Fig. 2 for the two growing seasons. A slightly drier than usual June, in 1971, was followed by a relatively normal, moist July and August; whereas, in 1972, June was moist, followed by an August-September drought. This resulted in a decline in tissue accumulation and plant cover during the last weeks of the summer of 1972 that contrasts with the continuous increase in total living biomass found in 1971.

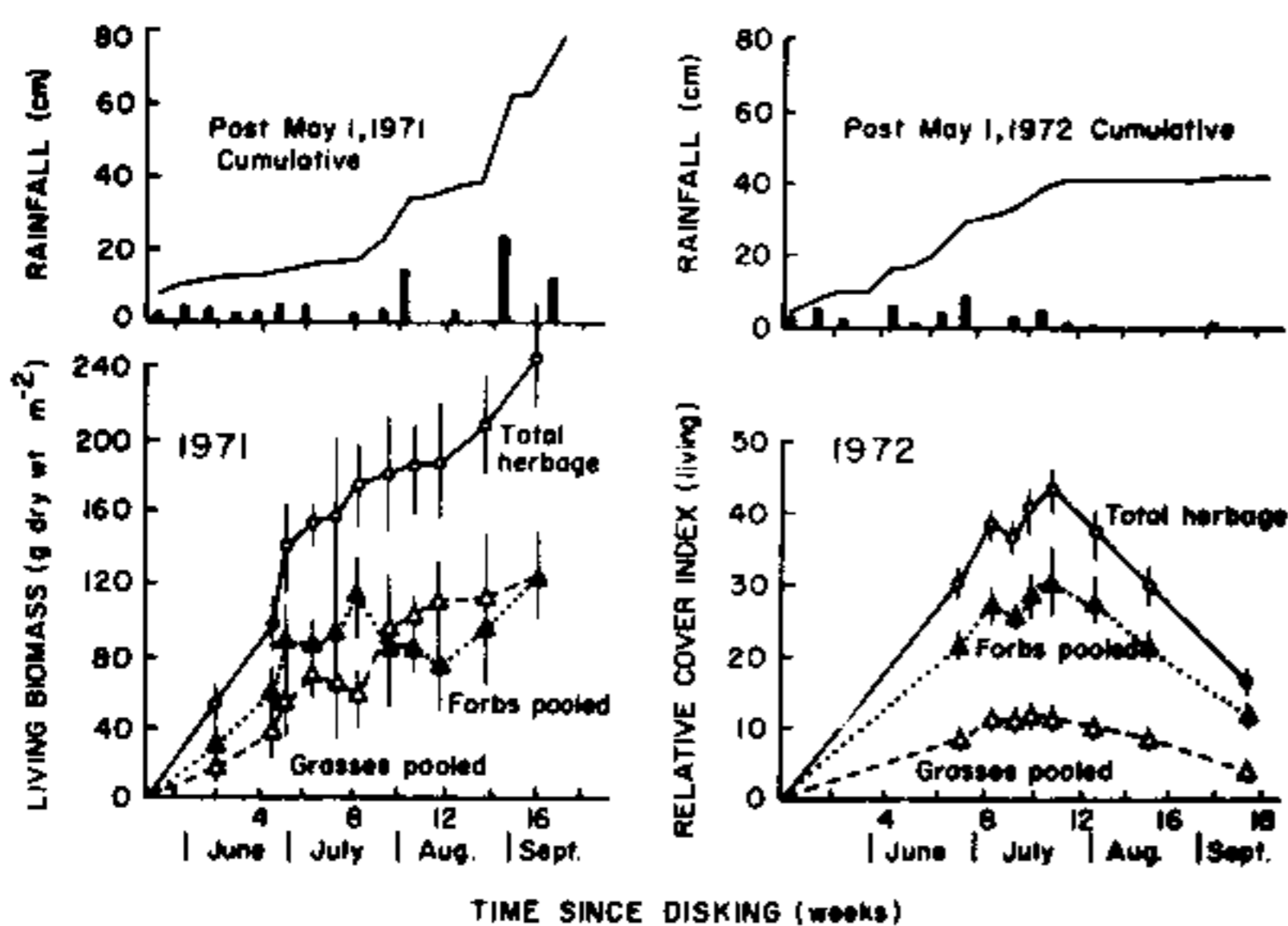


Fig. 2. Seasonal pattern of grass (Δ), forb (\blacktriangle), and total (\circ) living tissue in untreated control vegetation during 1971 and 1972, compared to the weekly rainfall and cumulative post-May 1 rainfall totals. Confidence intervals were calculated individually for each mean (95% C.I. = $\pm t_{.05}$ · standard error of the mean). The "relative cover index" is in arbitrary units of "number of hits for ten passages of a point through the vegetation."

Three types of growth patterns were evident for the individual species in 1971 (Fig. 3). *Raphanus raphanistrum*, an annual, reached an early season peak biomass and then died back after flowering during the month of June. *Convolvulus sepium* and *Agropyron repens*, both perennials, reached early season peaks and then maintained a relatively constant living biomass for the remainder of the summer. The late July *Agropyron* peak coincided with the time of seed set, and the subsequent slight reduction in biomass occurred following shattering and the loss of the caryopses from the clip samples. *Ambrosia artemi-*

siifolia initially grew at a much slower rate and achieved peak biomass in September when the experiments were terminated. Miscellaneous grasses (primarily species of *Setaria*, *Digitaria*, and *Panicum*) were not as important in the latter part of the 1972 season as they were in 1971. The most probable cause for this was the July and August drought. Other species included *Solanum carolinense*, which was frequent but patchy in occurrence; rare individuals of larger forbs (greater than 1 g dry wt per plant); and numerous perennial and biennial rosettes which did not contribute greatly to the living standing crop. The mean biomass of these other assorted forbs amounted to a maximum of 5.5 g dry wt · m⁻² on the 96th day after disking in late August, and therefore accounted for < 2% of the total biomass. Living plant cover totals declined during the late summer 1972 drought (Fig. 2), and this is reflected in the curves for all of the individual species groups (Fig. 3).

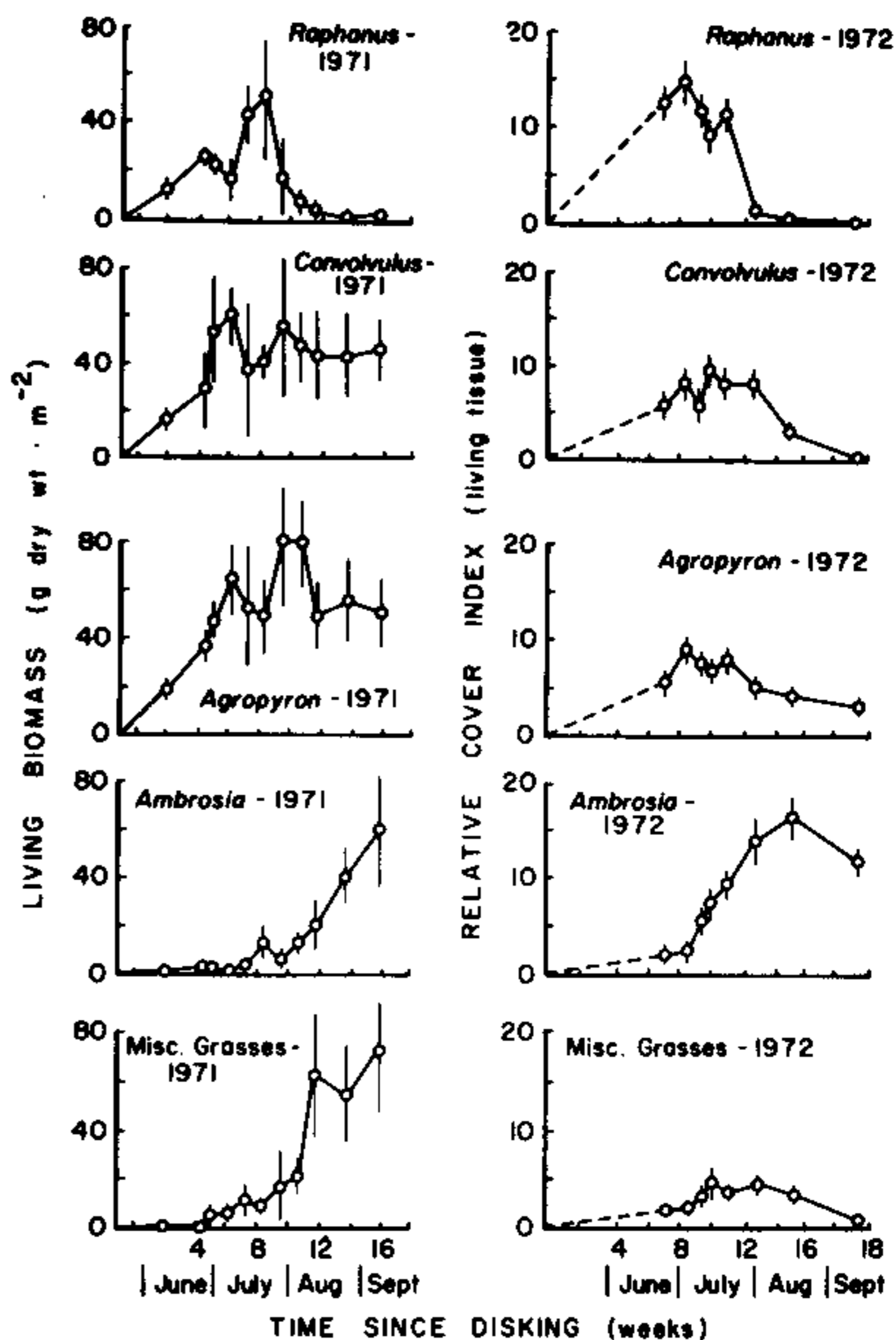


Fig. 3. Seasonal growth pattern of living tissue comprising the major species in 1971 and 1972. See Fig. 2 caption.

Response to a Single Disturbance at Different Times during the Growing Season

Sulfur dioxide fumigation at approximately 1 ppm applied for 4 hours in the morning was sufficient to bring about visible damage to the foliage of vegetation present in a first-year field. This was evident immediately after the termination of a fumigation, and, within 1 day subsequent to treatment, the lesions characteristic of SO₂ injury were apparent (Barrett and Benedict 1970). Separate statistical analysis of the data from the first fumigation period in mid-June during the 4th week after disking revealed highly significant reductions ($p < 0.01$) in living biomass of *Agropyron*, *Raphanus*, *Ambrosia*, the total forb component, and the total of all herbage. However, there was no significant reduction in living *Convolvulus*. The totals of combined living and dead tissues were unchanged except for *Ambrosia* and the grand total for all species, which were both significantly reduced ($p < 0.05$) (Cocking 1973).

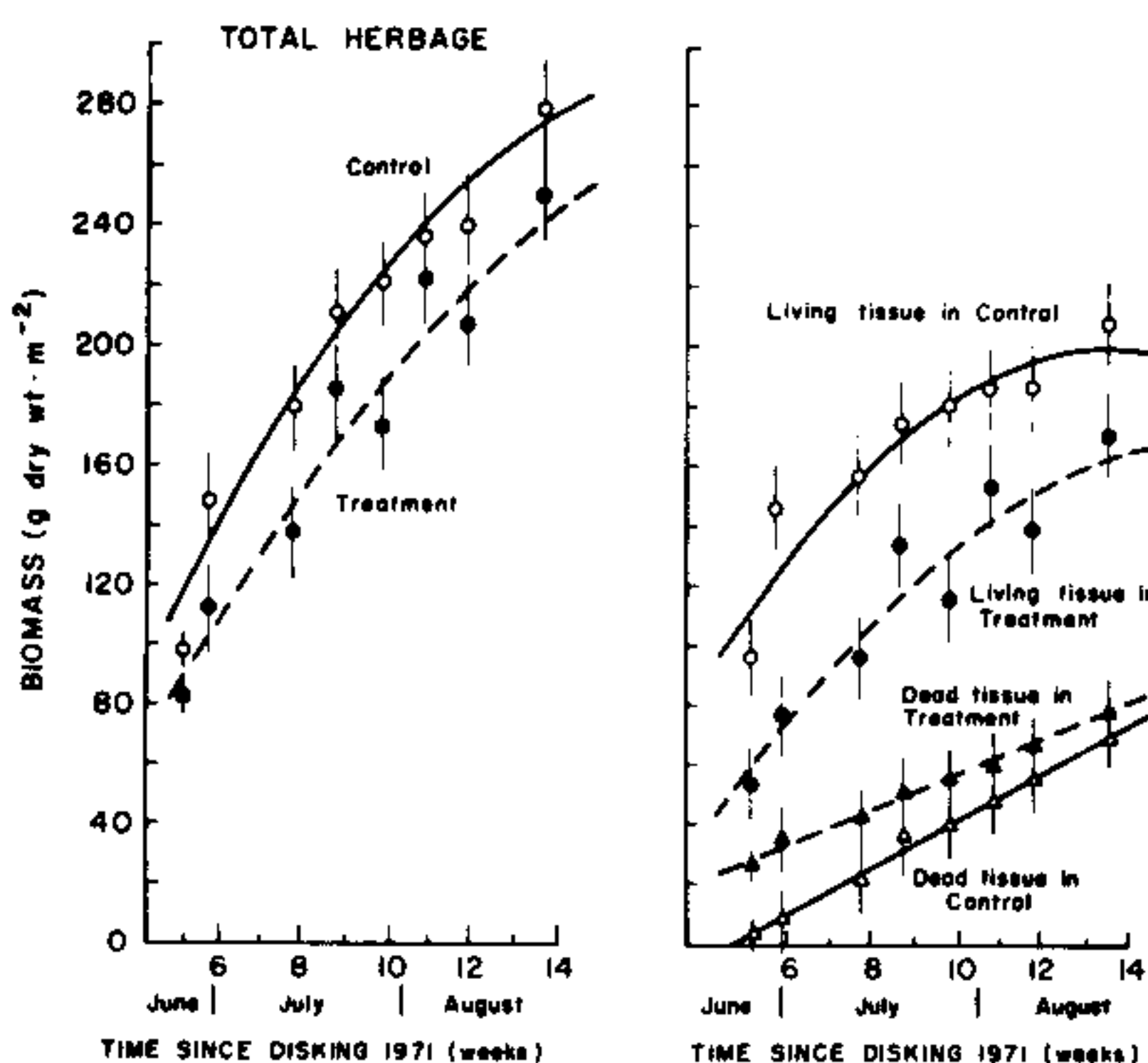
Similar results were obtained as a result of single experimental SO₂ fumigations applied during the balance of the 1971 growing season. The biomass of the total herbage and its apportionment into living and dead components in both control and previously disturbed (1 week earlier) vegetation is compared throughout the growing season in Fig. 4. The living biomass of the pooled grass and forb groups, as well as the major species groups, were treated similarly. *Agropyron*,

Raphanus, *Ambrosia*, *Convolvulus*, and the pooled living grass and forb components, as well as the total living herbage, all exhibited highly significant ($p < 0.001$) reductions in living biomass throughout the growing season. *Solanum* and the miscellaneous grasses did not appear to be significantly affected (Cocking 1973).

Percent necrosis, the percent of the total tissue of a particular component that was dead, was calculated for each clip sample. The values obtained were subjected to the same factorial ANOVAs used for the statistical analysis of the biomass data. There were significant ($p < 0.025$) differences in the percent necrosis of treated and untreated tissues of all taxonomic units, except for the grasses, that were dependent on the time of the disturbance during the growing season (Cocking 1973). In order to illustrate this interaction, a damage index was obtained by subtracting the mean percent necrosis in untreated control vegetation from that of a corresponding treated quadrat. If the resulting value exceeded the least significant difference (1sd_{.05}) determined from the pooled error mean square from the appropriate ANOVA, then the damage was also significant (Steele and Torrie 1960). Damage indices over the course of the growing season are presented in Fig. 5 for the grass and forb components of the plant community as well as for the total herbage. Highly significant regressions were obtained for each of these groups, demonstrating a decrease in the impact on the various components during the course of the summer. Individual species *Raphanus* and *Agropyron* showed similar declines (Fig. 6). *Ambrosia* and *Convolvulus* susceptibility was not dependent on the time during the season when the disturbance occurred, and individuals of these species showed significant damage throughout the summer. Conversely, the miscellaneous grasses did not exhibit significant damage at any time, and might, therefore, be classed as resistant. The decline in susceptibility of *Agropyron* implies a seasonal development of resistance, but the decline in *Raphanus* damage is probably the result of the lack of living leaf surface area resulting from normal seasonal death of this species (Fig. 3).

The 1971 experiment demonstrates that SO₂ causes a greater disturbance to a herbaceous plant community early in the growing season. This difference was not so much due to a change in the absolute reduction in living tissue, but to the fact that the damaged tissue represented a smaller proportion of the total photosynthetic biomass as the season progressed (Cocking 1973). Therefore, percent reduction in living standing crop is inadequate as a method for comparing the intensity of damage at different times during the growing season, since the same amount of damage can give a wide range of values depending on the amount of living tissue present prior to treatment. However, it is a measure of the relative impact on the system as an expression of the proportional loss of photosynthetic tissue.

Fig. 4. Total living and dead standing crop in control vegetation and after acute SO₂ disturbance, 1971. SO₂ treatment preceded each sample date by 7 days. Total herbage = living plus dead tissue (95% C.I. = \pm least significant interval = \pm 1sd_{.05}; $r^2 > 0.91$ for all curves).



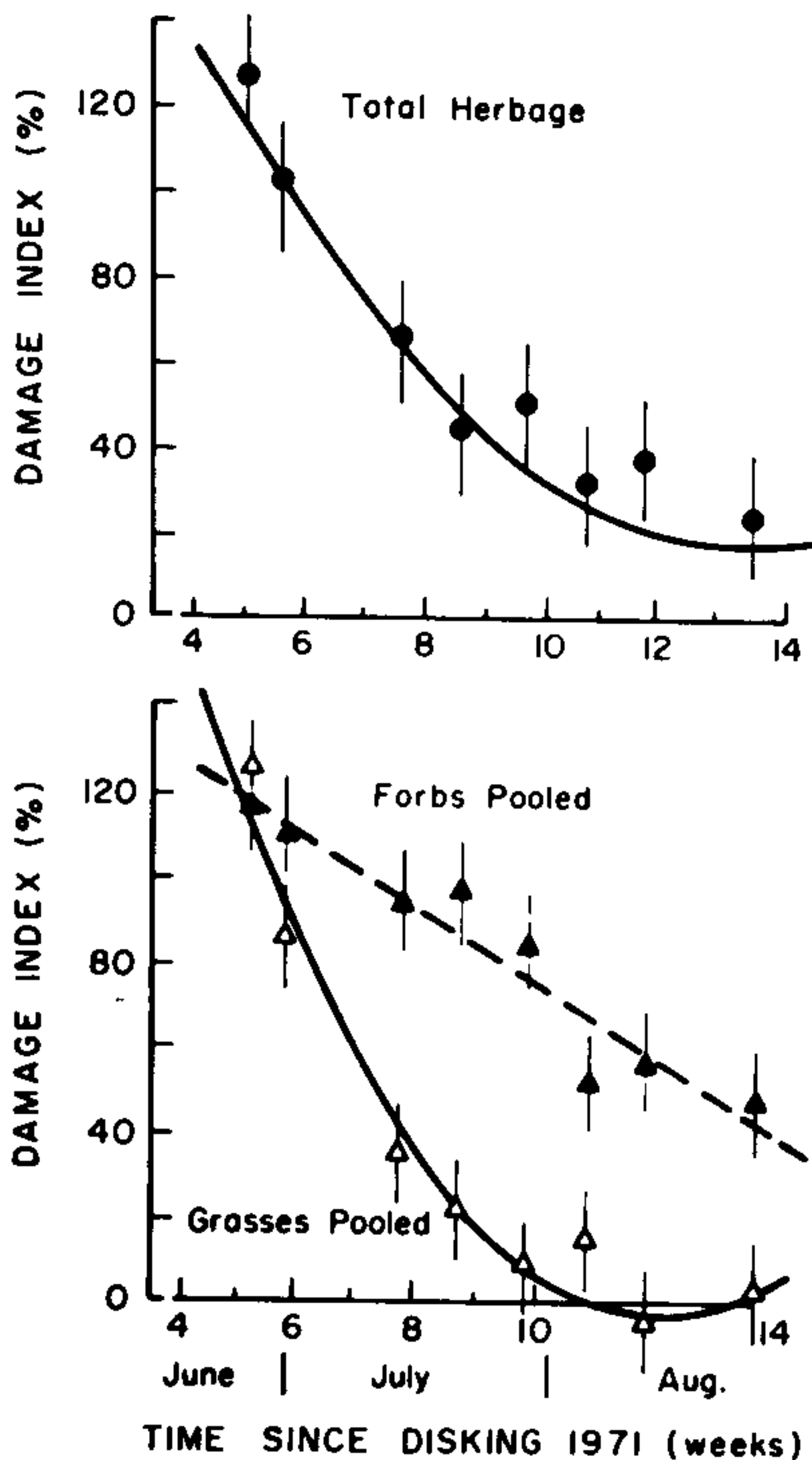
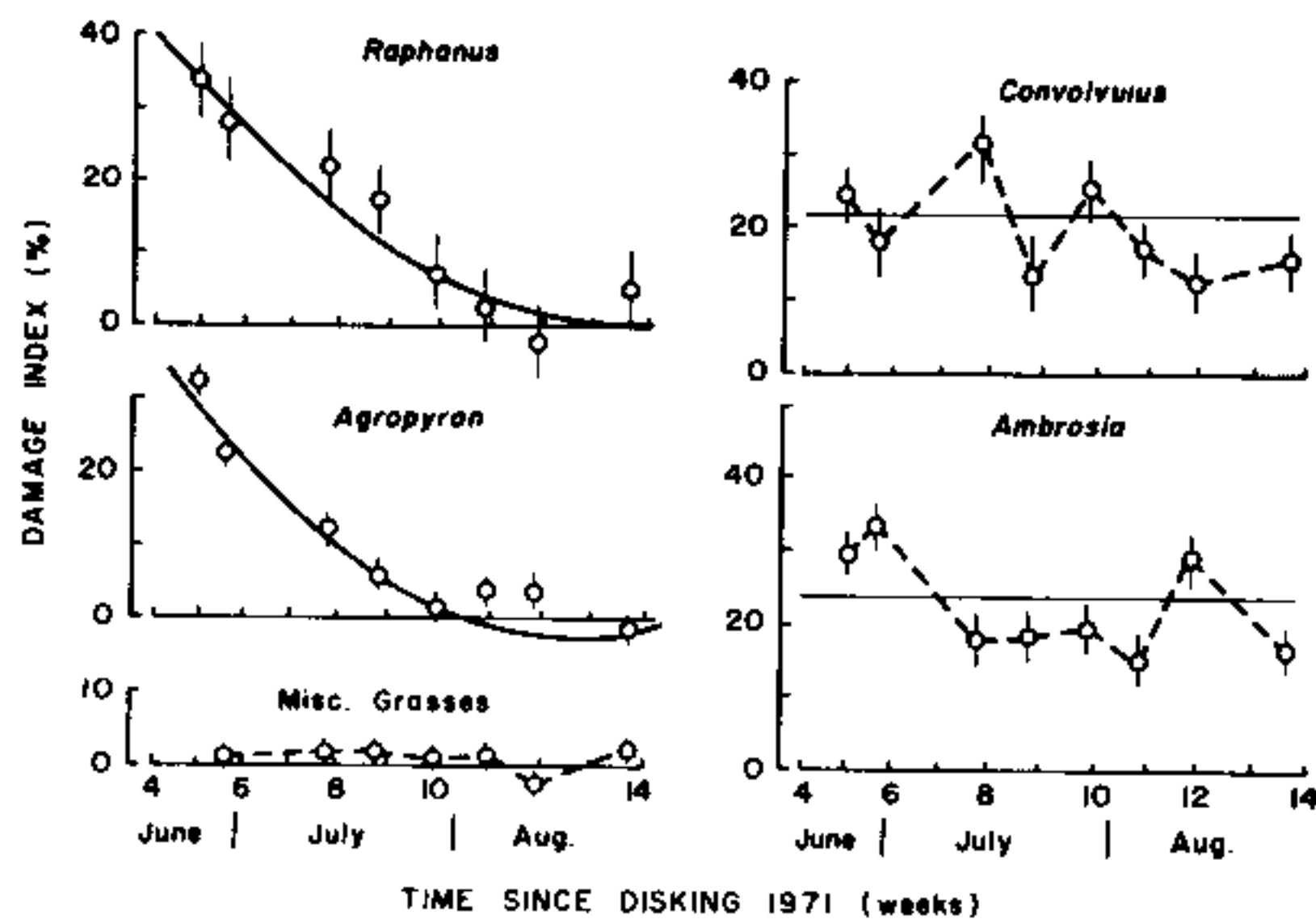


Fig. 5. Seasonal pattern of a damage index for the grass, forb, and total herbage 1 week following exposure to acute SO₂ disturbance, 1971. Damage index = percent necrosis in untreated herbage - percent necrosis in control herbage (95% C.I. = $\pm 1s_{i,0.05}$; $r^2 > 0.91$ for all curves).

The Effect of Prior Disturbance on Sulfur Dioxide Damage Intensity

In order to obtain a damage index of the same type calculated in 1971, the portion of dead tissue (percent necrosis) was calculated for each sample using the 1972 cover data. The percent necrosis of a plot sampled 24-48 hours prior to treatment was subtracted from that of the same plot 24-72 hours subsequent to treatment to evaluate the impact of SO₂ fumigations. The amount of damage from initial SO₂ treatment, and the additional

Fig. 6. Seasonal pattern of a damage index for the major species groups measured 1 week following exposure to acute SO₂ disturbance, 1971. Damage index = percent necrosis in treated herbage - percent necrosis in control herbage (95% C.I. = $\pm 1s_{i,0.05}$; $r^2 = > 0.92$ for *Raphanus* and *Agropyron*, n.s. for others).



damage from second treatments applied 3 or 15 days after the initial treatment, are summarized in Fig. 7. Significant damage ($p < .01$) occurred after the initial disturbance in all groups except the perennial rosettes. *Agropyron* was about ten times more susceptible than miscellaneous grasses which were damaged only slightly. *Ambrosia* and *Convolvulus* were more susceptible to the initial SO₂ treatment than *Raphanus*, and *Solanum* was the most resistant of the dominant forb species. Overall, the pooled forbs were twice as susceptible to a single disturbance as the grasses.

The interval length between disturbances affects susceptibility. Damage to total herbage after a short interval was only half that resulting from the initial treatment, while total herbage damage due to a second treatment applied one-half month after the first was 27% greater than that of the initial SO₂ fumigations (Fig. 7). This pattern of reduced impact shortly after the initial treatment is indicated for *Agropyron*, *Ambrosia*, *Convolvulus*, *Solanum*, perennial rosettes, and the pooled grass and forb groupings. In fact, negative damage indices were obtained in some cases, possibly as experimental error resulting from the small amount of living tissue on the sample date during the 3-day interval between the first and second disturbances, which served as pretreatment values in T2. In contrast, *Raphanus* was damaged again at a level comparable to that following the initial disturbance, regardless of the length of the intervening period. In summary, the response to a second disturbance is unique to each species, but in general, greater damage is caused to the system if there is a longer, one-half-month rather than a 3-day, interval between fumigations.

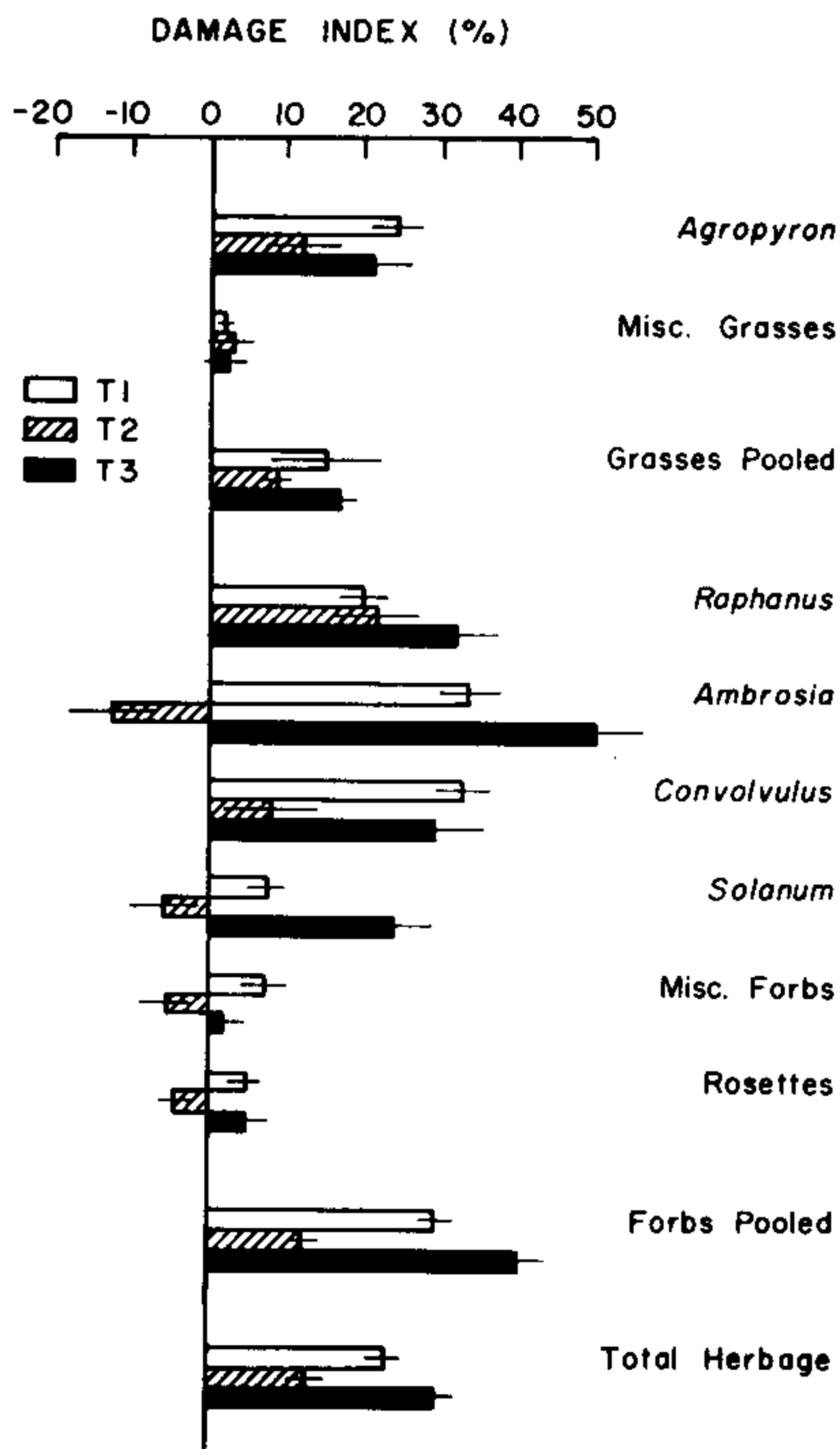


Fig. 7. Damage to previously undisturbed and previously disturbed vegetation. 1972. T1 = a single acute exposure to SO_2 ; T2 = damage due to a repeated SO_2 treatment on the 3rd day following an initial exposure; T3 = damage due to a repeated SO_2 treatment applied one-half month after an initial exposure. Damage index = percent necrosis in treated herbage - percent necrosis in control herbage (95% C.I. = $\pm 1.51 s_{i,0.05}$).

Community Recovery Following Single and Repeated Disturbances

The reduction in living tissue brought about by SO_2 fumigation does not persist for more than a few weeks following disturbance. Vegetation which was treated with a single fumigation in July and August 1971, during the 8th and 11th weeks, respectively, after disking, and the corresponding untreated quadrats were clip-

samped again at the end of the summer. In the second week of September, 13 weeks after disking, the mean total living biomass of the previously damaged vegetation ($251.9 \text{ g dry wt} \cdot \text{m}^{-2}$) was virtually identical to that of the undisturbed control vegetation ($247.8 \text{ g dry wt} \cdot \text{m}^{-2}$).

In 1972, relative cover of all living tissue in untreated vegetation over the course of the growing season was compared to that found in plots receiving single and repeated disturbances. The significant reductions in standing crop which occurred subsequent to each fumigation period again disappeared by September (Fig. 8). Control levels of vegetation cover were attained in the case of a single disturbance, T1, and exceeded in the case of repeated disturbances, T2 and T3.

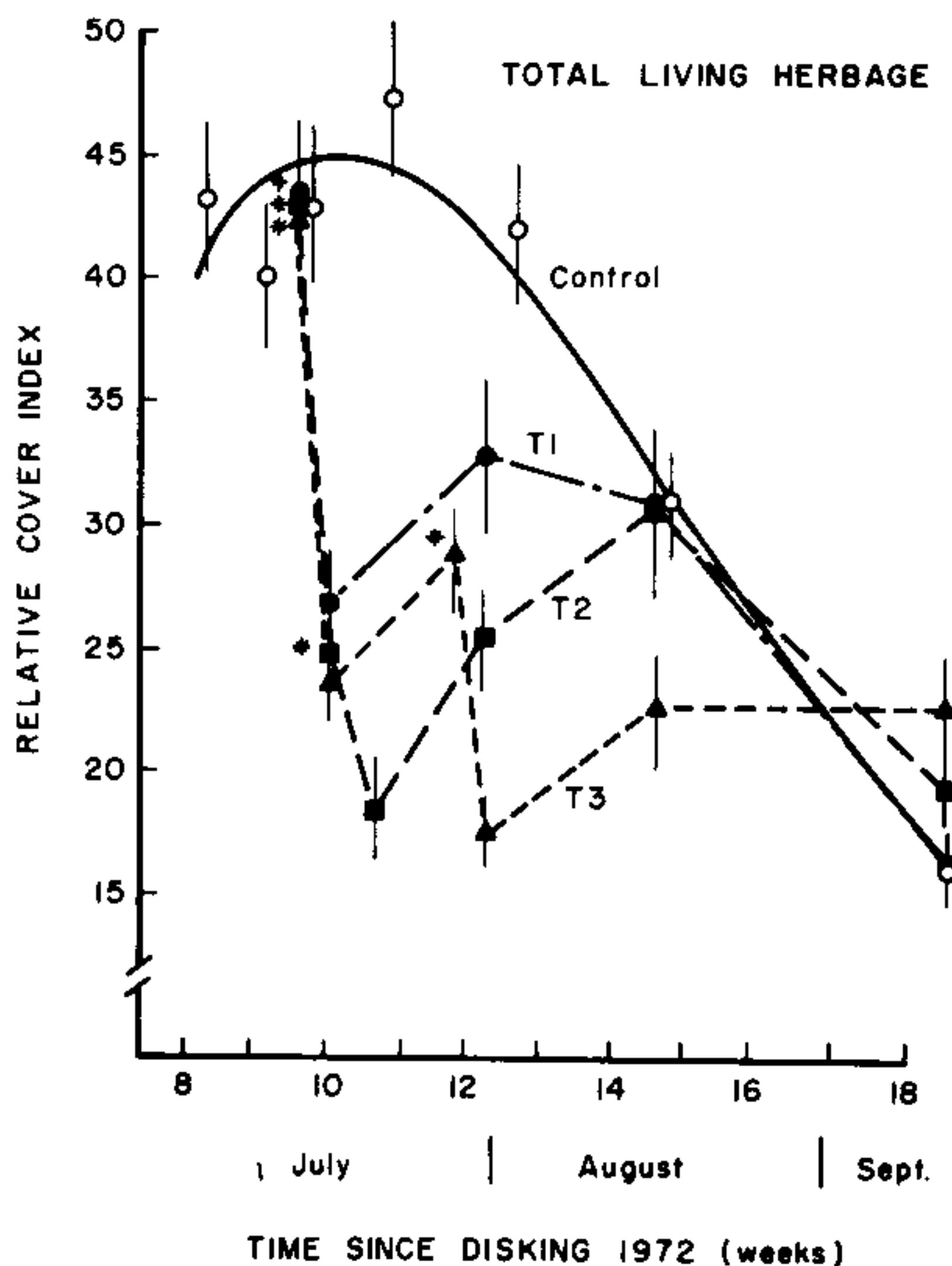


Fig. 8. Effect of single and repeated SO_2 disturbances on total living herbage. 1972. The "relative cover index" is in arbitrary units of "number of hits for ten passages of a point through the vegetation." (95% C.I. = $\pm t_{.05} \cdot \text{standard error of the mean}$; $r^2 = 0.94$ for control; $y = -140.45 + 6.17x - 0.06x^2$ for the control curve); \circ = untreated control; \bullet = T1, a single acute SO_2 disturbance; \blacksquare = T2, two acute SO_2 disturbances, 3 days apart; \blacktriangle = T3, two acute SO_2 disturbances, one-half month apart. SO_2 treatment followed within 3 days of the sample indicated by "*".

The miscellaneous grass component was not damaged significantly by repeated disturbance (Fig. 7), and by the end of the growing season there was over twice as much grass in plots treated previously than in untreated vegetation (Fig. 9) due primarily to increases in *Setaria*, *Digitaria*, and *Panicum*. *Agropyron* contributed little to the recovery process (Cocking 1973). In contrast, forb cover, which was reduced extensively subsequent to each fumigation, never returned to levels attained in untreated vegetation (Fig. 10). This differential response occurred under the summer drought conditions which reduced growth in both forbs and grasses in untreated vegetation (Fig. 3).

The percent composition of grass and forb species in each sample is presented in Fig. 11. During week 10 there was approximately 25% grass in the living component of the untreated vegetation, and there were no significant changes in this ratio during the remainder of the growing season. Significant increases in the grass component occurred subsequent to all three treatment regimes. A single treatment increased the grass to 50% of the herbage by early September, and the most severe disturbance, two treatments one-half month apart, resulted in vegetation that was over 60% grass. By the end of the growing season, *Ambrosia* made up 94% of the control forb component and 90, 80, and 87% of the forbs in treatments T1, T2, and T3, respectively. *Convolvulus*, which was important in the repair process during 1971, was not significant in 1972 due to its slow growth in all plots as a result of the August-September drought conditions.

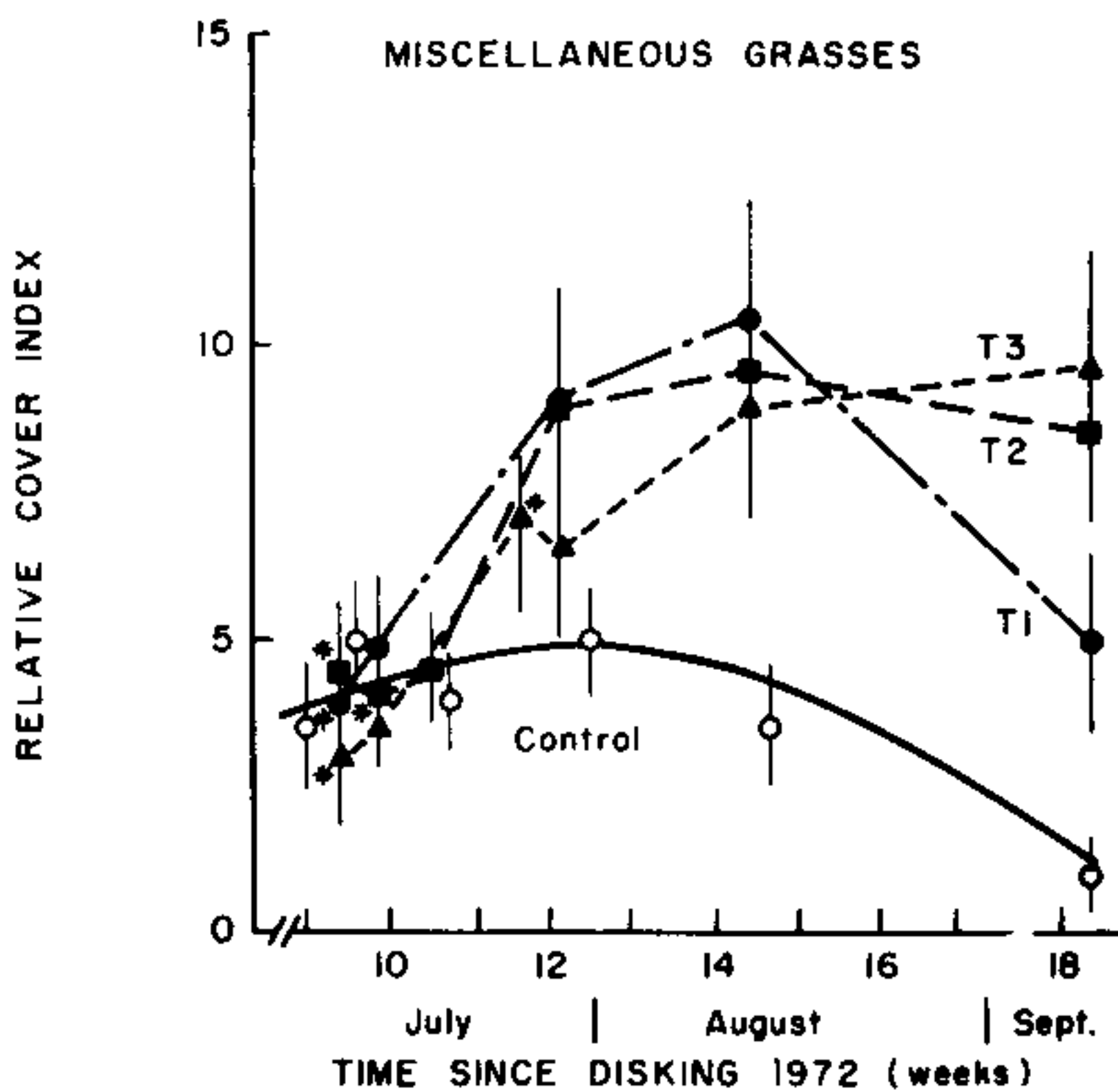


Fig. 9. Effect of single and repeated SO₂ disturbances on the miscellaneous grasses. 1972. See Fig. 8 caption. For the control curve $y = -9.312 + 0.317x - 0.002x^2$; $r^2 = 0.83$.

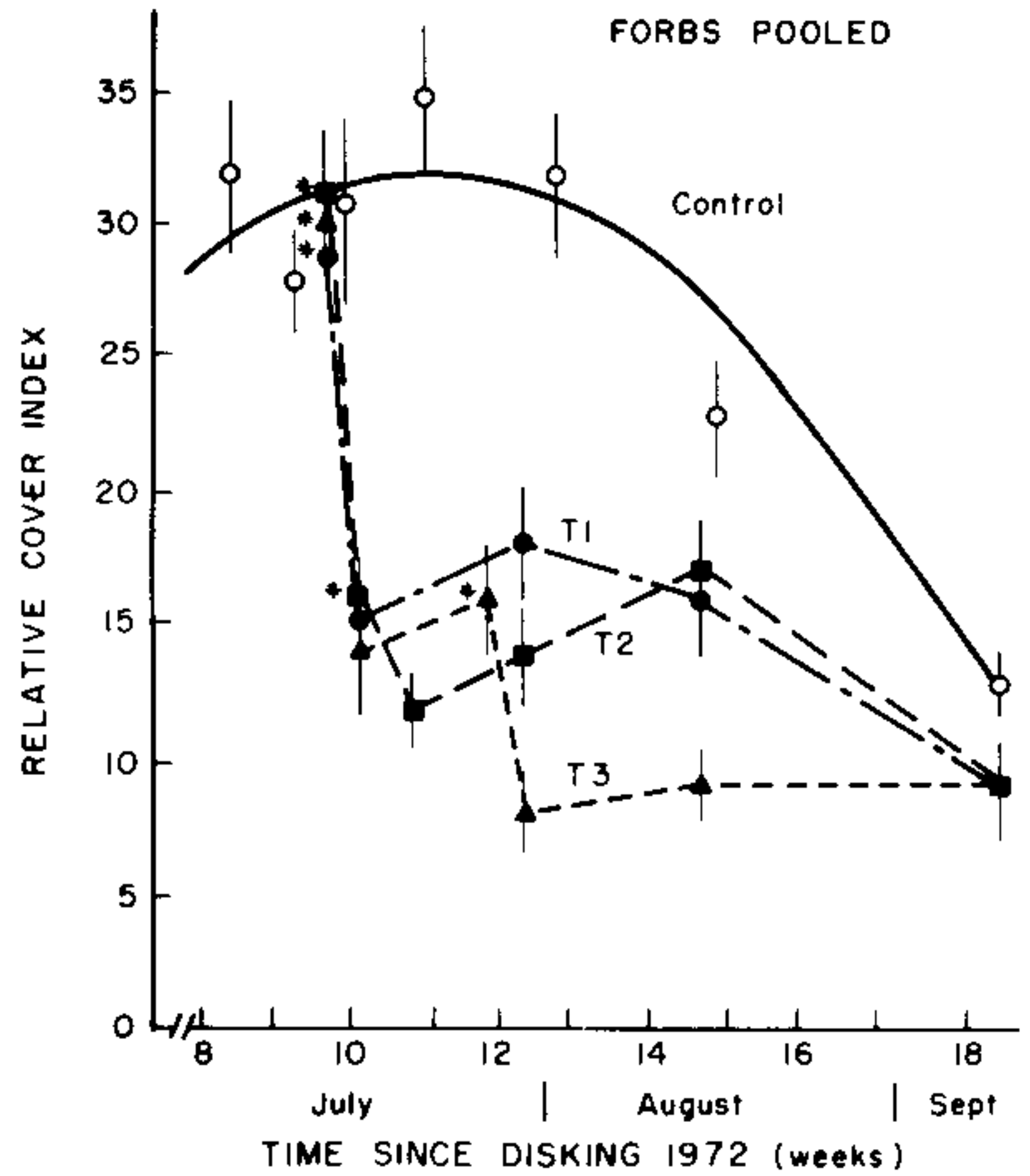
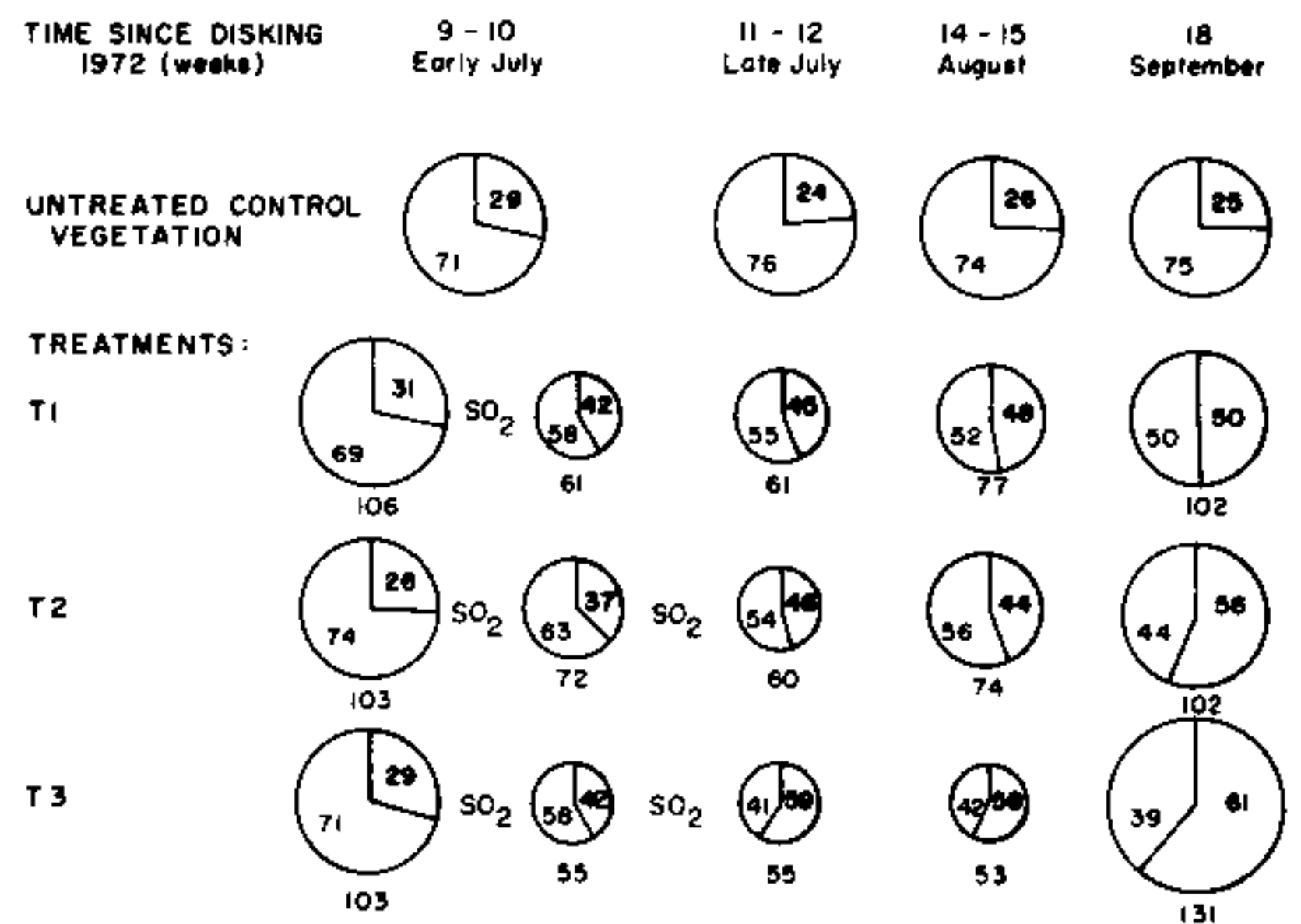


Fig. 10. Effect of single and repeated SO₂ disturbances on the pooled forbs. 1972. See Fig. 8 caption. For the control curve $y = -12.85 + 1.13x - 0.007x^2$; $r^2 = 0.86$.

Fig. 11. Percent composition of grasses (left side) and forbs (right side) in untreated control vegetation compared to that receiving a single acute SO₂ disturbance, T1; two acute disturbances 3 days apart, T2; and two acute disturbances one-half month apart, T3. 1972. The occurrence of a disturbance between samples is indicated by "SO₂." The size of the circles is proportional to amount of plant cover in the treated vegetation expressed as a percentage of that in the control herbage. The numerical percentage is immediately below the circle.



Discussion

Patterns of Susceptibility to SO₂ Disturbance

Damage occurring in response to experimental SO₂ fumigation was evident by the end of a 4-hour treatment period, and necrotic lesions developed fully within 24 hours. Acute tissue injury of this type has been reviewed by Thomas and Hendricks (1956), Thomas (1961), Brandt and Heck (1968), Daines (1968), and Mudd and Kozlowski (1975). Individual susceptibility varied greatly, and leaves from adjacent plants of the same species, as well as individual leaves on the same plant, responded differently to the same disturbance. Varietal differences in sensitivity to atmospheric pollution have been recognized, and the occurrence of plasticity within natural populations is common (Sinclair 1969, Gabelman 1970, Smith 1972). Ambient SO₂ levels measured at Hutcheson Memorial Forest were less than 0.03 ppm, and these first-year communities had probably been exposed to minimal acute SO₂ pollution prior to this experimental work. The variability in the response of individuals to fumigation indicates a population history involving little selection pressure for resistance to SO₂. The research site is located in a part of New Jersey that is potentially exposed to atmospheric pollution of many forms including ozone, nitrogen oxides, and various exotic industrial effluents. Any or all of these could have been present during the experimental periods and acted synergistically with SO₂. These were not monitored during this study and must be considered to be part of the experimental error and a potential source of additional variability.

Setterstrom and Zimmerman (1939) found that recently expanded, mature leaves were the most susceptible to SO₂ damage. They indicated that older leaves would tend to be less susceptible, and this may be one of the reasons for late season resistance of *Agropyron* since little new growth occurred during August and September (Fig. 3). Setterstrom and Zimmerman (1939) also indicated that the young leaves surrounding the apical meristem were the most resistant, and this was particularly true for *Ambrosia*. Resistance of very young leaves has been attributed to the lack of fully functional stomata, which are the pathway for gas entry into the plant (Thomas et al. 1950, Daines 1968). Resistance of the forb apical meristem to SO₂ damage is important to the plant community in that continued growth is possible subsequent to relatively severe disturbance. For example, the recovery pattern observed in 1972 would have been significantly altered if *Ambrosia*, the dominant forb at the end of the growing season, had been completely killed, rather than defoliated with the apical meristem still intact. Similarly, the grasses recovered because damage, if it occurred, was generally restricted to the leaf tips, and the meristems, near the ground at the base of the sheaths (Esau 1965), were unaffected.

Environmental conditions at the time of SO₂ disturbance affect the intensity of damage (Setterstrom and

Zimmerman 1939, Daines 1968, Treshow 1970). Even though statistically significant differences correlating with fumigation conditions were not obtained in this study, subjective observation indicated that they did occur. The plants were visibly more affected on days characterized by high humidity, late morning dew on the foliage, and high soil moisture content than when a hot early morning sun had dried vegetation. The absence of correlations indicates that these differences were absorbed in the overall experimental error of this study.

The field as a whole was more readily damaged in June than in August (Fig. 5). Except for *Convolvulus*, which was susceptible throughout the growing season, the greatest sensitivity to SO₂ damage occurred during the period of vegetative growth prior to flowering. In the case of *Ambrosia*, this resulted in a sensitivity throughout the entire growing season, whereas *Agropyron*, for example, showed increased resistance to SO₂ throughout the summer and was not damaged following the late July flowering and seed set (Fig. 10).

The group of miscellaneous grasses, including species of *Setaria*, *Digitaria*, and a small amount of *Panicum*, were the most resistant plants throughout the growing season. They were not significantly damaged in the 1971 experiment (Fig. 6) and were only slightly damaged by the initial 1972 fumigations (Fig. 7).

Evidence to explain the erratic occurrence of significant differences in the susceptibility of *Ambrosia* and *Convolvulus* is circumstantial. *Convolvulus* demonstrated a significantly lower resistance around day 54 of 1971, while *Ambrosia* was responding with average sensitivity in terms of the entire growing season. Then on day 83, *Ambrosia* was highly susceptible while *Convolvulus* was more resistant (Fig. 10). The lack of correlation between the susceptible and resistant periods of these two species indicates that the differences may be due to intrinsic properties of the species rather than the environmental conditions at the time of fumigation. The slope of the growth curves (Fig. 3) indicates that the control vegetation growth rates of both species were high, thereby producing more recently expanded susceptible leaves at the time of high sensitivity.

Difficulties inherent in attempting to list relative susceptibilities of plants, such as the classical ratings of O'Gara cited by Thomas et al. (1950), those of Benedict and Breen (1955), and others cited by Wood (1968), are obvious from the data presented in Fig. 6. For example, on the first of July it would be reasonable to rate *Raphanus* and *Agropyron* as considerably more susceptible than *Convolvulus*. However, by mid-July (Fig. 10), the ratings are completely reversed. Therefore, even if the fumigation conditions are carefully controlled and defined, the extension of quantitative ratings to field estimates of conditions responsible for damage must be carried out with caution and a thorough understanding of community phenology.

An interesting aspect of the damage pattern for total herbage is evident from Fig. 12. The percent necrosis for total herbage within plots treated 1 week prior to sampling remains constant throughout the growing season, while the percent necrosis in control plots continually increases due to normal seasonal die-back. The percent necrosis linear regression of control plots intercepts the mean percent necrosis of treatment plots (30.3%) on day 106. This would indicate that a fumigation of 1 ppm for 4 hours is unlikely to affect the system significantly toward the end of the growing season. Only one SO₂ level was used in the 1971 experiment. Therefore, there is no evidence to support the presence of similar constants at other levels of disturbance, even though they may exist. It does seem reasonable, however, to hypothesize that decreasing intensities of disturbance would affect the system for shorter and shorter periods early in the growing season. This is supported by Leone et al. (1965) in their study of factors influencing SO₂ phytotoxicity in New Jersey. They showed that even though optimum environmental conditions and SO₂ concentrations for inducing damage occur in both spring and fall, most of the damage observed in the field occurs early in the year following the spring burst of new growth. In addition, they found that SO₂ concentrations high enough to produce characteristic lesions were relatively rare during the summer months.

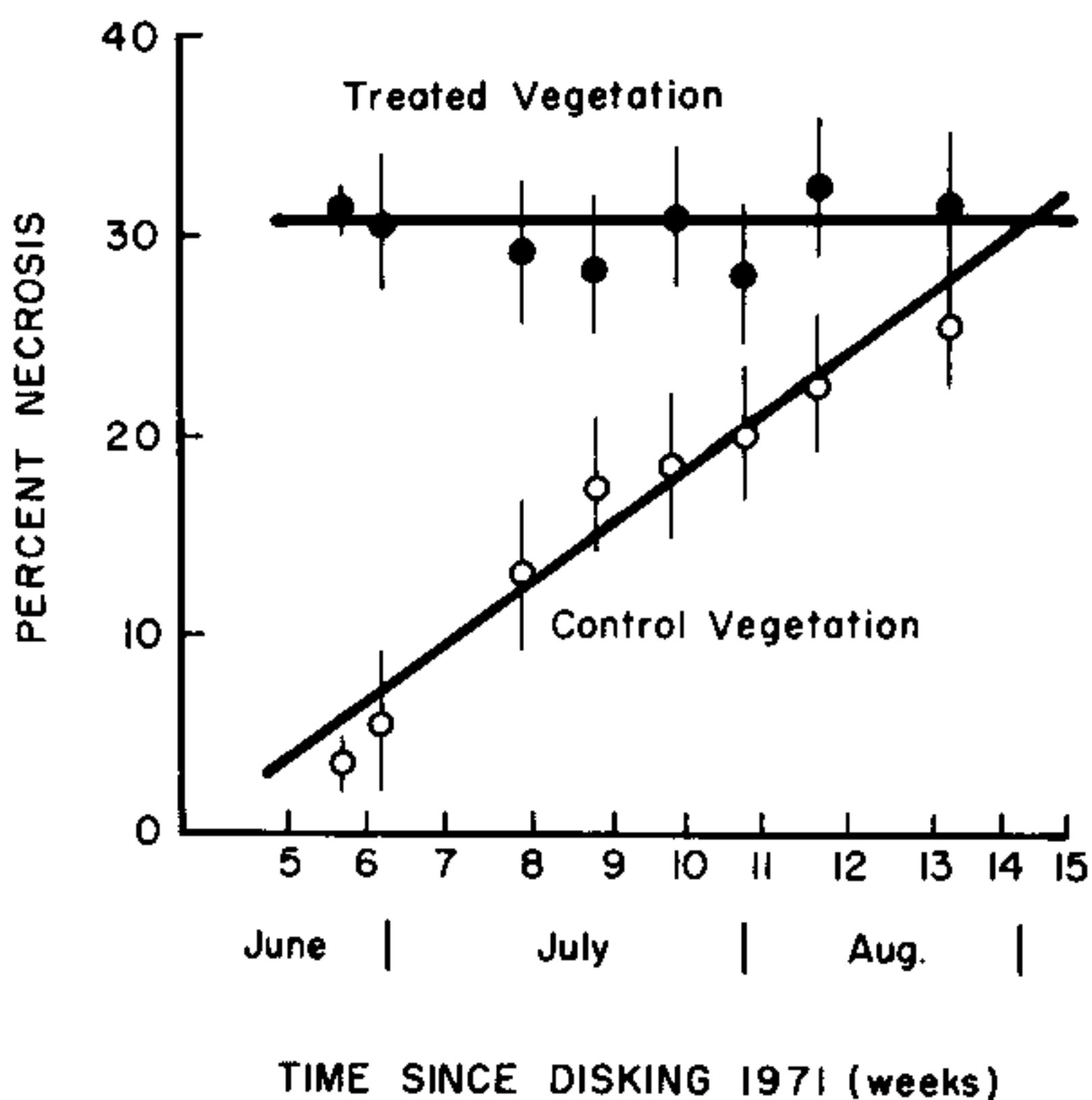


Fig. 12. Percent necrosis of total herbage in 1971 treated (●) and control (○) vegetation. SO₂ disturbance occurred 1 week prior to the sampling date in the treated herbage (95% C.I. = $\pm 1s_{i,0.05}$; for control vegetation $y = -8.016 + 0.370x$; $r^2 = 0.96$).

One of Smith's (1972) recommendations was that experimental studies should be made with realistic levels of atmospheric pollution. There is no real ecological value to investigations carried out with concentrations several times higher than those that are obtained in the field. The choice of 1 ppm for 4 hours was made with this principle in mind. This concentration is well above ambient conditions in "unpolluted" regions, exceeds chronic damage levels, and is also above the goals for air pollution control established by state and federal agencies (Wood 1968); however, it is not above levels that have been observed in the field prior to federal regulation of allowable sulfur content of fossil fuels. For example, the 8-hour maximum in Chicago, Illinois, during 1964 was 1.02 ppm and the 24-hour maximum during the same period was 0.79 ppm (Middleton 1969). This along with a potential relaxation in current standards leads to the conclusion that the stress used was realistic, that damage of the intensities observed in this study is attainable in natural ecosystems, and that the subsequent impact needs to be evaluated.

Effect of a Second Disturbance

Time-concentration relationships have been established for SO₂ (Thomas and Hendricks 1956, Thomas 1961, Daines 1968) that indicate additional damage will occur if the same concentration is applied for an increased number of hours. In this study the effects of repeated fumigations of the same level and duration, 1 ppm for 4 hours, applied after short or long undisturbed periods, were examined. The total plant community was further damaged by a second exposure to SO₂ after both short and long intervals. Damage from a treatment regime involving two fumigations was defined as the sum of the damage indices (Fig. 7) for the initial and subsequent disturbances. The overall impact, and the proportional impact of a second fumigation, are summarized for each taxonomic grouping in Table 1. When the second disturbance occurred after a brief interval, the impact on total herbage was 39.2% of that due to the initial perturbation. However, when the fumigations were separated by one-half month, the impact of the second disturbance was 99.7% of that due to the first. Therefore, when the total damage is used as a measure of community impact, a second perturbation after a short interval increases the amplitude of a pulse occurring at essentially one point during the growing season, but more widely spaced disturbances increase the total amount of tissue damage from SO₂. This is probably a result of the time available for the regrowth of foliage through the expansion of leaves close to the apical meristem, which were initially resistant, into more susceptible, recently matured leaves.

The three hypotheses posed in the introduction concerning the impact of repeated disturbances may now be evaluated in terms of these results. The first, that a disturbance would weaken the system and allow greater damage by a second fumigation, was not supported. The initial fumigation did not induce greater

susceptibility to an immediate recurrence of a similar SO₂ exposure. In some cases, individual species such as *Ambrosia*, *Raphanus*, and *Solanum* were more susceptible to SO₂ damage after the longer, one-half-month interval (Table 1), but seasonal differences in resistance and fumigation conditions may have been determining factors. There is no evidence to link the increase with a "weakening" of the resistance of the system. Treshow (1968) and Sinclair (1969) have cited various instances where plant communities damaged by air pollutants have been found to be more susceptible to other environmental stresses or disturbances such as fungal infections and insect invasions.

The second hypothesis, that the system would be more resistant to a second disturbance, is supported in the case of short-interval repeated fumigations but is refuted for those occurring after an interval sufficient for some regrowth of the vegetation.

The third hypothesis, that subsequent fumigations will damage the system independent of the previous history, is refuted by the results of the short-interval,

repeated-disturbance experiment and cannot be supported or refuted on the basis of damage due to perturbations which were one-half month apart. It appears that damage is dependent to a large extent on the history of the plant community, and more extensive study of this aspect of the response to disturbance is warranted.

Community Repairability and Resiliency

Holling (1973) indicates that resiliency is the "persistence of relationships within a system" and that systems can be "very resilient and still fluctuate greatly, i.e., have low stability." These terms were defined in the context of population fluctuations but may also be used to describe the behavior of any measurable level in the system. Initial plant tissue damage is only one aspect of the impact on the total system. Loss of living tissue in itself would not be as important if the replacement of this damaged material did not require an energy expenditure on the part of the system and if the material that was

Table 1. Total damage due to single and repeated disturbances to first-year old-field vegetation.
(ns = no significant increase in damage over initial treatment [$p < 0.05$])

Species	Initial damage (%)	Total damage with a brief interval (%)	Second stress impact as % of interval	Total damage with a ½-month interval (%)	Second stress impact as % of initial
<i>Agropyron</i>	22.6	33.8	49.4	43.2	90.9
Miscellaneous grasses	1.3	ns	ns	ns	ns
Pooled grasses	14.0	22.5	60.2	29.5	110.6
<i>Raphanus</i>	18.4	38.8	111.0	49.4	168.6
<i>Ambrosia</i>	32.0	ns	ns	80.2	150.5
<i>Convolvulus</i>	31.6	39.9	26.2	60.2	90.4
<i>Solanum</i>	6.9	ns	ns	29.4	323.9
Miscellaneous forbs	6.4	ns	ns	ns	ns
Perennial rosettes	4.2	ns	ns	ns	ns
Pooled forbs	31.7	43.7	37.6	70.4	121.9
Total herbage	28.1	39.1	39.2	56.1	99.7

being replaced (primarily leaves) was not itself the major site of energy conversion and entry into the system. Therefore, the pattern of replacement of photosynthetically active plant tissue is a measure of the efficiency of the community in minimizing the impact of the disturbance, and the magnitude of loss which can be endured with the system persisting is one measure of resiliency. Vogel (1980) gives many examples of systems which respond favorably to disruption and which are resilient in this sense of the definition. The difficulty of evaluating resilience and stability in natural ecosystems which are, for the most part, not at equilibrium and characterized by constant ground states but which change temporarily (McIntosh 1980, Allen and Forman 1976) within a dynamic environment (Holling 1973, Innis 1976, Forman and Boerner 1981), is well known.

The control vegetation curve in Fig. 8 may be considered as the changing ground state for the plant community as a whole (Hurd et al. 1971, Allen and Forman 1976) and the pulse reduction and recovery of living plant cover can be compared to it. The rapidity of the response to the disturbance is indicated by the length of time required to reach maximum deflection, and the damping time is measured by the length of time from maximum deflection until the function intercepts the "control" ground state. The intensity of the response to disturbance is reflected in the amplitude of the deflection from ground state. The damping times for total density plant cover regrowth following a single disturbance and two disturbances over a brief interval are virtually identical (Fig. 8). This indicates that recovery from the more severe pulse must have been the result of a greater overall rate of repair while the more widely spaced disturbances increased the damping time and prolonged recovery.

The third objective of this study was to determine whether system self-regulation was the result of increased growth rates, changes in species composition, or a combination of both mechanisms. Shifts in species composition with an ascendancy in the importance of grasses have been shown (Fig. 11). The growth rates of treated and untreated vegetation of all species groups and the various plant community compartments were calculated using the IBM Continuous System Modeling Program, CSMP (IBM 1969). Mean cover values, such as those presented in Figs. 8, 9, and 10, were used to define time-dependent AFGEN functions of control and treatment (T1, T2, and T3) vegetation cover in a CSMP model. In order to determine the growth rates, the AFGEN-produced functions of living cover indices were differentiated using the CSMP DERIV function, and the rates were then divided by the standing living cover index at each iteration producing a specific growth rate (change in living cover \cdot time $^{-1}$ \cdot standing living cover $^{-1}$ = $\Delta x/x \Delta t$). Three critical dates were chosen during the recovery period: Day 80 was subsequent to the entire stress of T1 and T2 but

before the second stress of T3; day 95 was shortly after the second stress of T3; and day 110 was representative of a date late in the recovery period for T1 and T2 and during the peak recovery period for T3.

The specific growth rate of the control vegetation on these dates was subtracted from that of the treatments to determine a net growth rate. Forb, grass, and total plant community growth rates increased in response to the treatments (Fig. 13). A very high growth rate increased grass cover immediately following two closely spaced fumigations, T2; however, the difference between the growth rates of control and treated vegetation disappeared by day 110 in the quadrats which received a single fumigation, T1, and had decreased somewhat in the quadrats which were disturbed twice, T2 and T3.

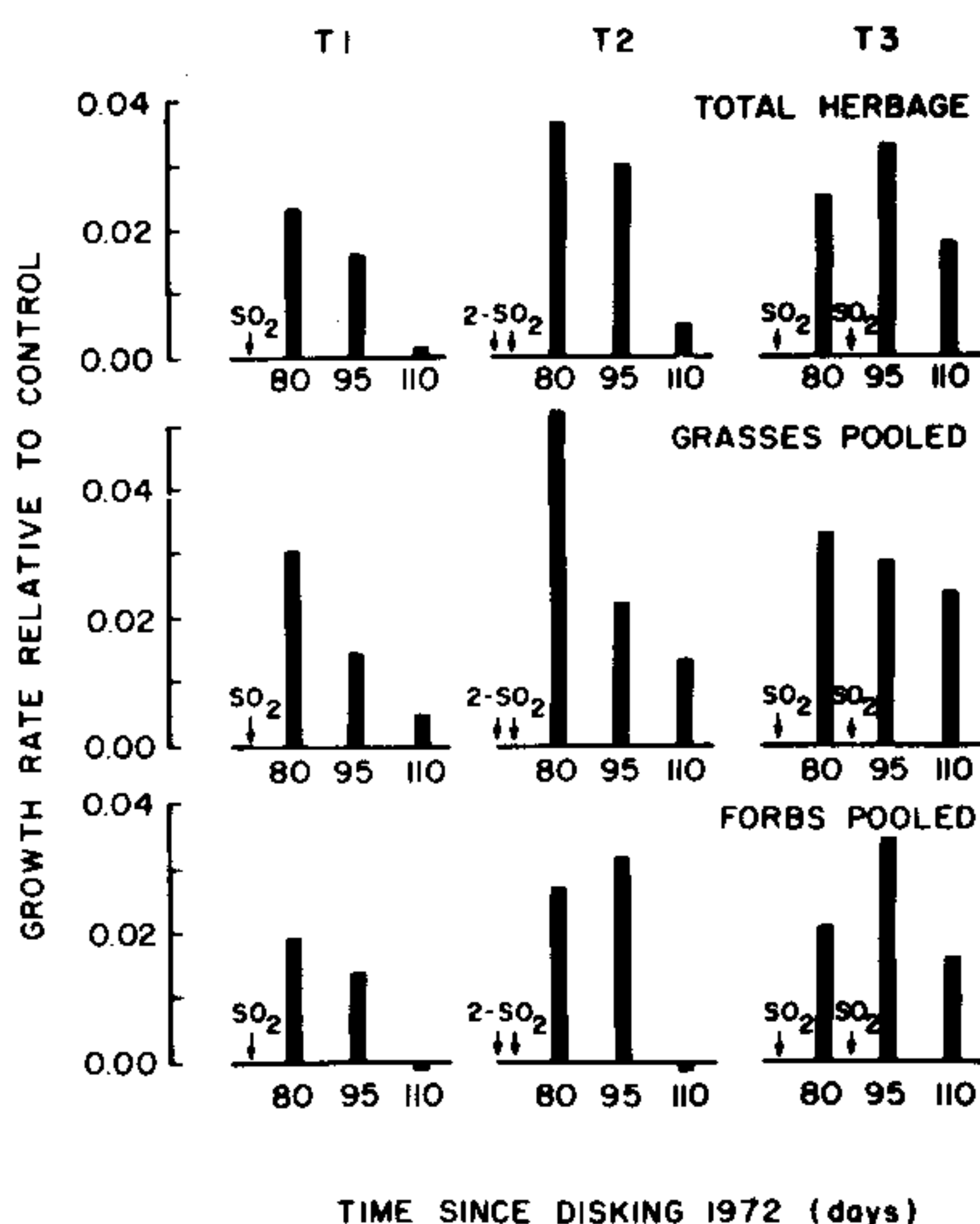


Fig. 13. Differences in specific growth rates of total herbage, pooled grasses, and pooled forbs as compared to those in untreated control vegetation on days 80, 95, and 110 during the period of recovery following disturbances which occurred either once, SO₂, or twice, 2-SO₂, within the 15-day period prior to the sampling date. T1 was a single acute disturbance by SO₂, and T2 and T3 were two disturbances which occurred 3 days and one-half month apart, respectively. The "growth rate relative to the control" is the "change in living cover index/day/current standing living cover index on the day treated."

Therefore, recovery in this system was due to a combination of increases in specific growth rates (Fig. 13) and changes in species composition (Fig. 11) brought about by shifts in competitive advantages which occurred as a result of the greater susceptibility of forbs to SO₂ stress than grasses (Fig. 7). This finding is compatible with the shifts in composition of older fallow fields (Allen and Forman 1976), of mixed forage cultures observed by Guderian (1967), the early observations of Hedgecock (1914) of shifts toward grassland species in the more severely damaged areas around the Ducktown and Copper Hill Smelters of Tennessee, and the persistent species near the SO₂-producing iron-sintering plant at Wawa, Ontario (Gordon and Gorham 1963).

Impact on the Potential for Energy Conversion

The extent of the disturbance to vegetation can be estimated by quantifying the extent and duration of the loss of photosynthetically active tissue through the production of necrotic lesions. Daines (1968) demonstrated that regrowth of necrotic tissue must occur to

reestablish normal assimilation rates. The previously discussed measures of damage do not reflect the total disturbance to the ecosystem over time. In order to obtain a measure of cumulative photosynthetic potential, the amount of living chlorophyll-pigmented tissue, as estimated by the daily cover index of treatment and control vegetation, was summed over an extended portion of the 1972 growing season. This value, which is indicative of the energy-converting capacity of the plant community during the period, was calculated over the interval from day 68 to day 130, using the CSMP INTGRL function. The difference (\bar{d}) between these values is a measure of the reduction or increase in photosynthetic potential (in tissue-cover days) during that interval. Negative values indicate deleterious effects, and positive values show that the disturbance was stimulatory and produced more photosynthetic surface than that found in undisturbed vegetation (Cocking 1973). This difference can also be expressed as a percent change from that of untreated control vegetation ($\% \bar{d}$), and these values for the component parts of the plant community are presented in Table 2.

Table 2. Change in photosynthetic potential of the plant community during the interval between day 68 and day 130 as a result of SO₂ disturbance. \bar{d} = the difference in living cover-tissue days between treated and untreated vegetation. $\% \bar{d}$ = \bar{d} /living cover-tissue days of the untreated vegetation.

Species	T1 One stress		T2 Two stresses closely spaced		T3 Two stresses ½ month apart	
	$\% \bar{d}$	\bar{d}	$\% \bar{d}$	\bar{d}	$\% \bar{d}$	\bar{d}
<i>Agropyron</i>	-3.7	-12	-29.4	-93	-6.7	-21
Miscellaneous grasses	+133.8	+283	+137.1	+290	+125.4	+265
Pooled grasses	+51.4	+271	+37.3	+197	+46.2	+244
<i>Raphanus</i>	-49.8	-83	-31.5	-53	-56.8	-95
<i>Ambrosia</i>	-43.1	-360	-53.7	-488	-64.0	-534
<i>Convolvulus</i>	-35.5	-105	-56.6	-168	-60.4	-180
<i>Solanum</i>	-27.2	-28	+53.0	+55	-36.4	-37
Miscellaneous forbs	-18.0	-8	-27.2	-12	-56.3	-24
Perennial rosettes	-37.0	-43	-58.9	-68	-28.5	-33
Pooled forbs	-40.2	-627	-44.5	-694	-57.9	-904
All herbage	-17.0	-356	-23.8	-497	-31.6	-660

Increases in total grass and, except in the case of *Solanum*, decreases in the photosynthetic surface area of all forbs occurred during the balance of the growing season in all treatments (Table 2).

The relative difference statistics ($\% \bar{d}$) for total cover of the plant community give an index of the impact on the entire plant community following the disturbance. These values can be used as a quantitative answer to the question posed at the outset concerning the relative impact of two stresses applied over different intervals of time. The 32% reduction in photosynthetic potential of the entire plant community as a result of the more widely spaced disturbances (T3) places a 37% greater impact on the entire system than the 24% reduction due to the more closely spaced disturbances (T2). In addition, the smaller (17%) reduction following a single treatment confirms the expected result that a single disturbance (T1) will produce less impact than repeated disturbances.

This index is only an approximation of the photosynthetic potential. All living tissue (leaves, stems, fruit, and flowers) above the soil level was included in the relative cover index, and the photosynthetic rates and efficiencies of these tissues differ greatly as do those of the different species. The bulk of the miscellaneous grasses in this study carry on C_4 carbon fixation (Smith and Brown 1973) and are therefore efficient energy fixers (Black 1971). The overall deficit in photosynthetic surface area may therefore be offset by increased metabolic efficiency and thereby moderate the impact on the system as a whole.

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