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## REVIEW AND ASSESSMENT OF VARIOUS TECHNIQUES FOR ESTIMATING NET AERIAL PRIMARY PRODUCTION IN GRASSLANDS FROM HARVEST DATA[1]

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## I. INTRODUCTION

One of the major objectives of the International Biological Program (IBP) is to assess the net primary production of various ecosystems as a functional property of the system, which then should provide the base of the energy flow among various trophic levels. Consequently, numerous studies of primary production of grasslands have been undertaken in a number of countries; and in a majority of these, data on the time series harvests of biomass form the basis of computing the net production. However, no single standard technique of computation is available which would give comparable estimates across grassland types; and hence various authors have used different techniques. Recently Singh and Yadava (1974) applied four different techniques to the same set of harvest data and came up with widely different estimates of net aerial production. Consequently , various techniques should be reviewed and tested on comparable sets of harvest data collected under a coordinated sampling program from different grassland types.

This exercise should address questions, such as: (*1*) Does any one technique give highest (or lowest) estimates across various grassland types or on the same type in different years? (*2*) To what degree do estimates obtained from one technique differ from those obtained from other techniques applied to the same set of data? (*3*) Is the additional time-input justified in going from a simple procedure which gives a lower estimate to a more elaborate one giving a higher estimate? (*4*) What are the implications of using different methods in cross-site interpretation and synthesis of results? (*5*) Do simple conversion factors exist which can be applied to the estimate obtained by one technique and make it comparable to the estimates obtained by the other techniques?

Fortunately, data from 1 to 3 years from 10 widely distributed US grasslands with paired grazed and ungrazed treatments were collected in a comparable fashion under the auspices of US/IBP Grassland Biome Program. We, therefore, applied a number of techniques to these data sets in order to answer the questions raised above. The results of this study along with a review of published methods are reported in this paper.

## II. REVIEW OF PUBLISHED METHODS

Standing crop of the aboveground plant material is the primary variable that is measured when harvest techniques for estimating aboveground net production (ANP) are employed. Standing crop refers to the weight of the plant material present in the system at a given instant in time. Biological productivity, on the other hand, is a continuous process so it is necessary to designate a time unit (Odum, 1971); for example, the total amount of dry matter elaborated in the aboveground plant parts of a grassland during the whole year is its

annual net aerial production. Therefore the terms "standing crop" and "production" are not synonymous, and indeed production is estimated from the standing crop values in several ways when harvest technique is used.

The easiest method that has been used to estimate ANP is simply to measure total weight of the standing vegetation at the end of the growing season (Hadley & Kieckhefer, 1963; Kucera, Dahlman, & Koelling, 1967). However, by the time this measurement is taken at the end of the growing season, a significant amount of material produced may have senesced, detached, and disappeared from the recognizable vegetation. A modification of the method that increases the amount of field work required and, hopefully, accuracy involves frequent harvests of total standing crop and equating the season's peak value with ANP of the growing season or the year (Bray, Lawrence, & Pearson, 1959; Hadley & Buccos, 1967; Lester, 1969; Malone, 1968; McNaughton, 1968). This assumes that there is no carry-over of standing crop biomass from one season to another. Ovington, Heitkamp, and Lawrence (1963) estimated ANP by subtracting the lowest measured overwintering weight from the season's peak biomass to allow for the carry-over growth. Singh (1968) found that in tropical grasslands in India three distinct growth periods could be distinguished. To obtain an estimate of ANP within each growth period, the standing crop values at the beginning of the growth periods were subtracted from the peak values. The annual net production was then the sum of these three seasonal production values.

Odum (1960) pointed out that in old fields in South Carolina ANP is always greater than peak standing crop because not all species in the community simultaneously reach their peak biomass. He also emphasized that as succession proceeds, total standing crop becomes less an estimate of ANP because of the increased diversity. For these reasons he used a method to estimate ANP that involved frequent harvests and summation of the peak live weights of individual species. The ratio of total standing crop to ANP ranged from 0.9 the first year after abandonment to less than 0.6 the seventh year. He considered his estimates of ANP minimal because he did not consider herbivory or senescence during a sample interval. Singh and Yadava (1972, 1974) subtracted the biomass value of the first sampling date from the sum of species peaks to account for the carry-over herbage.

Malone (1968) reported results of a study designed to compare the peak standing crop method with the summation of species peaks method. He found in three 1-year-old field ecosystems that the peak standing crop method consistently underestimated ANP. However, a larger error term was associated with the summation of species peaks method, ranging from 16% to 18% of estimates, compared to 7% to 11% for the peak standing crop method. He also determined that the difference between the two methods decreased as the phenologies of the dominant producers became more similar. Lauenroth (1970)

found in a northern mixed-grass prairie that the summation of species peaks gave an estimate of ANP that differed by only 7% from the peak standing crop.

Pearson (1965) estimated net production in grazed and ungrazed desert communities containing both shrubby and herbaceous components by summing the annual increments of the major species. Annual increments were calculated by dividing the average growing season standing crop by the average age of the species. However, estimation of the age of individuals in a field is very difficult, and also the standing crop in situations where there is rapid turnover of aerial parts may give no indication of the annual increment.

Lauenroth (1973), in an attempt to resolve the problem presented by the large variances usually associated with summing up peak biomasses of individual species, grouped various species into functional groups on the basis of their growth behavior during the growing season (i.e., warm season grasses, cool season grasses, etc.). The values of peak standing crop of species groups were then summed to give the estimate of total production of the growing season.

The summation of peaks by species to represent ANP assumes that each species peaks only once in the season. However, Singh (1968) demonstrated that certain species may show more than one peak. Kelley, Van Dyne, and Harris (1974) also recognized that the time series trace of species biomass may not be a monotonically increasing function and any method that accounts for only one peak for a species may be seriously underestimating ANP. They therefore proposed to sum the positive increments in biomass by species or species groups. They found in eight different communities that the average increases in the estimate of ANP over the peak standing crop method were: 41% by the summation of single species peak method; 94% by summing all positive increments in biomass by species; and 79% by summing only those increments for which the biomass estimates by species were significantly different ($\alpha = 0.05$). They also pointed out that the estimates of ANP by the summation of species peaks were lower when the sampling interval was increased from 1 week to 4 weeks by as much as 59%. This reduction in estimate was a function of two factors, a reduction in the number of species detected and the increased probability of missing positive biomass increment. Kennedy (1972), in a study designed to compare the ANP estimates from peak standing crop, sum of species peaks, and sum of positive increments by species, found that the latter method yielded highest estimates. This conforms with the observations of Kelley et al. (1974). However, the summation of positive increments by species is more sensitive to sampling variability, and a larger number of samples is needed to reduce this variability and increase the precision of the estimate (Kelley et al., 1974).

In these methods the material that died and was detached from the shoots before the species peaks were observed is ignored. Golley (1965) estimated the transfer from live to dead compartment in a broom sedge community and added this quantity to the sum of peaks for broom sedge and forbs in order to estimate the net production.

Wiegert and Evans (1964) suggested a paired plot method to estimate the disappearance of dead material over short intervals and equations to calculate senescence during these intervals. They argued that if in a homogeneous area of vegetation a pair of quadrats of the same size are located and if the dead material on one of these is removed at time zero ($t_0$) and weighed ($w_0$) and later at time one ($t_1$) the dead material on the second quadrat is removed and weighed ($W_1$), the disappearance rate of dead material ($r_i$) in $g \cdot g \cdot day^{-1}$ is given by:

$$r_i = \frac{\ln (w_0/w_1)}{(t_1 - t_0)}. \tag{1}$$

To minimize errors the quadrats were chosen so they shared one border, and the one to be clipped at $t_0$ was chosen at random. Also at $t_0$ the live vegetation on the second quadrat was removed to reduce errors from additions to the dead material. Total standing crop of live aboveground vegetation was sampled at intervals during the growing season.

ANP was then calculated in the following way.

Let:

$t_i$ = a time interval in days

$a_i$-1 = standing crop of dead material at start

$a_i$ = standing crop of dead material at end

$b_i$-1 = standing crop of green material at start

$b_i$ = standing crop of green material at end

$r_i$ = instantaneous daily rate of disappearance of dead material during the time interval

$x_i$ = amount of dead material disappearing during an interval

Then:

$$x_i = \frac{(a_i + a_{i-1})}{2} \cdot r_i \, t_i \tag{2}$$

$$\Delta b_i = b_i - b_{i-1} \tag{3}$$

and a change in green standing crop,

$$\Delta a_i = a_i - a_{i-1} \tag{4}$$

a change in dead standing crop. Therefore, the mortality of green material during the interval ($d_i$) is given by

$$d_i = x_i + \Delta a_i \tag{5}$$

Equation (5) has the restriction that $d_i$ must be $\geqslant 0$. ANP is then estimated by

$$ANP = \sum_{i=1}^{n} (\Delta b_i + d_i) \tag{6}$$

where n = number of intervals sampled. They reported an increase in estimates of ANP for two sites ranging from 2.5 to 4.9 times greater than peak standing crop. They further argued that for stable ecosystems net biomass accumulation is zero during an annual period and that ANP should be equal to the annual amount of dead material disappearing.

Lauenroth (1970) applied the above method to a mixed-grass prairie site and found that the transfer of live material to the dead during the growing season was 101% of ANP estimated by summing the species peak biomasses. Estimates of mortality in $g \cdot m^{-2} \cdot day^{-1}$ ranged from 6.68 to 0.72. The data were extremely variable; the second of the pair of quadrats in some cases had more dead material on it at the end of the interval than the first quadrat had at the start. This points out the near impossibility of locating two identical areas of dead material in a mixed species community. Another problem encountered was regrowth and senescence within the second quadrat during the interval. Also many of the calculations in this method are executed using milligrams and tenths of milligrams which are questionable when using harvest data. Furthermore the method assumes that since stable ecosystems do not accumulate biomass over the year, ANP can be estimated by the disappearance of dead material for the year. This assumption, i.e., stable ecosystems achieve an exact carbon balance each year, may not necessarily be the case for many ecosystems (Lester, 1969).

Lomnicki, Bandola, and Jankowska (1968) suggested a modification of the Wiegert and Evans (1964) method of estimating senescence and ANP. At time $t_0$ live vegetation is removed from one of the plots ($b_0$), and from the other plots all dead material is removed. At time $t_1$ both live ($b_1$) and dead material are collected from this latter plot. The increase in the amount of dead material between $t_0$ and $t_1$ represents mortality ($h_i$). ANP is then calculated by equation (7):

$$ANP = \sum_{i=1}^{n} (h_i + \Delta b_i) \tag{7}$$

where $h_i$ = the mortality during interval i and $\triangle b_i$ = the increase in live biomass for the same interval.

Although this modification may reduce the field work, the previous criticisms of Wiegert and Evans (1964) also apply here.

Wallentinus (1973) further modified the method of Wiegert and Evans (1964) and did away with the necessity of paired quadrats. The single quadrat method produced values 31% larger than the peak biomass plus current dead and 17% greater than the sum of species peaks (live and current dead).

All methods which sum biomass peaks on a species or species group basis or sum the positive increments in biomass by species run a risk of assuming a "mythical community." In a time series of standing crop data, variations in space are often greater for individual species than variations over time. Whenever the variation in space within sampling intervals is large relative to the trend over time, the summation of peak standing crops creates a "mythical community" in which all groups presumably appear at the highest indicated standing crop on a composite square meter of ground. The problem increases with the increase in the number of groups and sampling frequency (D. N. Hyder, personal communication). According to Sims and Singh (1971), in situations where a greater species diversity exists, the sum of species peaks method may lead to an overestimation because of the tendency to overestimate the species occurring in small amounts.

Another point that needs emphasis here concerns the limitation of species biomass data. It is often difficult to determine the biomass of each species in a multispecies community with an acceptable degree of precision (Lauenroth, 1973). It is possible to use some statistical criteria such as a requirement that the species biomass on sample dates adjacent to the peak must be significantly less than the peak; otherwise, they must be averaged. This may mitigate some of the criticisms.

Several other techniques not using data on individual species biomass have been recently suggested. Milner and Hughes (1970) suggested a method for calculating ANP using total live biomass.

$$\text{ANP} = \sum_{i=1}^{n} (\triangle B_i) \tag{8}$$

where $\triangle B_i$ = the change in the live biomass during the $i^{th}$ interval. They also point out that these calculations do not consider mortality during the growing period and suggest the method of Wiegert and Evans (1964) for estimating this. Instead of summing up the positive increments in the live biomass only, Singh and Yadava (1972) summed the positive increments in the total standing crop (live + dead + litter). They called this a minimal estimate of ANP because if the growth in the live component occurred concomitant with the

decomposition in the litter compartment, it would not show up in the calculation. The sum of positive increments in the live biomass only is also an underestimation because the growth that senesced during the sampling intervals is not accounted for. For this reason, in a later paper Singh and Yadava (1974) estimated ANP by summing the positive increments in aboveground live biomass and the positive increments in the standing dead material if both increments occurred concomitantly. The last sum was included to account for mortality during sampling intervals. This method produced estimates of ANP 18% larger than the method of summing the positive difference in total standing crop (live + standing dead + litter), 11% less than the summation of the species peaks and 66% less than the summation of positive increments in biomass by species. They felt that the consideration of positive increments by species overestimates the production and carries large error terms.

Lewis (1970) proposed a very comprehensive scheme for calculating ANP which he termed balance sheet approach. In this method, net primary production (NPP) for any year is given by the following relation:

$$NPP = \sum_{i=1}^{n} P_{gi} - (R_{ai} - R_{bi}) = AA_i + AB_i \qquad (9)$$

where $P_{gi}$ = gross photosynthesis, $R_{ai}$ = aboveground respiration, $R_{bi}$ = belowground respiration, $AA_i$ = aboveground net assimilation, and $AB_i$ = belowground net assimilation. The net assimilation aboveground (AA) is calculated as follows:

$$AA = \sum_{i=1}^{n} (\Delta SC_i + \Delta r_i + \alpha Ph_i + \beta D_i + \gamma SS_i + \delta Ex_i + \epsilon H_i \pm \zeta T_i + \eta TD_i + \theta FM_i) \qquad (10)$$

where $\Delta SC_i$ = the change in standing crop of live material since the last sample and $\Delta r_i$ = the change in residue of live material not included in $\Delta SC_i$. Total live biomass produced in a year is then equal to the sum of $\Delta SC_i$ and $\Delta r_i$ over all intervals i. The remaining terms in equation (10) are transfers from net production. The lower case Greek letters represent transfer coefficients. $\alpha Ph_i$ = the transfer of nutrients to phyllosphere organisms, $\beta D_i$ = the same to disease organisms, $\gamma SS_i$ = the same to sap-sucking organisms, $\delta Ex_i$ = transfers to the atmosphere as gases or the soil as leachates, $\epsilon H_i$ = translocation grazing, seed-collecting, or stem-boring organisms, $\zeta T_i$ = translocation to or from aboveground organs, $\eta TD_i$ = the same to organs which have senesced, and $\theta FM_i$ = transfers to litter as a result of cutting, trampling, or weathering.

It is clear that the author intended this method to be comprehensive, but at the same time this intention resulted in it not being practical. Application of the method will require making the assumption that all terms in equation (7) after $\triangle SC_i$ are negligible, reducing it to:

$$AA = \sum_{i=1}^{n} \triangle SC_i \qquad (11)$$

III. APPLICATION OF METHODS ON COMPARABLE DATA SETS

## A. Background on the Data Used

The sites from which the present sets of data were collected are located between 30° and 50°N latitudes and longitudes 95° to 120°W (Table I). Elevations range from 390 m (ALE) to 2340 m (Bridger) above mean sea level. These sites represent Pacific Northwest bunchgrass (ALE and Bison), high mountain (Bridger), mixedgrass prairie (Cottonwood, Dickinson, and Hays), tallgrass prairie (Osage), shortgrass prairie (Pantex and Pawnee), and desert grassland (Jornada) types.

Annual precipitation at the sites ranged from a low of 158 mm for the ALE Site in 1972 to a high of 984 mm for the Bridger Site in 1970. Growing season precipitation (precipitation received during the period when the 15-day running mean air temperature $\geqslant 4.4°C$) was highest for the tallgrass prairie site (Osage) in 1971 and lowest for the Pacific Northwest bunchgrass site (ALE) in 1971 (Table I).

The mountain grassland site at Bridger had consistently lower average growing season temperatures than the other sites, and Osage, the tallgrass prairie site, had the highest average growing season temperature.

The experimental design at each site involved an ungrazed and a grazed treatment with two replicates of each. The ungrazed treatment refers to relatively long-term exclusion of large domestic herbivores with the exception of Jornada where the exclosure was erected on a lightly grazed area. The grazed treatment refers to grazing during the previous growing season, but not while sampling was conducted. The exception to this was Pawnee 1970 and ALE both years where sampling and grazing were concurrent. Grazing was by cattle and in most cases could be described as moderate. Further details of climate, soil, community structure, herbage dynamics, and trophic relations of the sites are available in Rasmussen (1971), Reuss (1971), Risser (1971), Sims and Singh (1971), and Lewis (1971), respectively.

Aboveground biomass on all the sites was estimated by the harvest technique. Harvest frequencies were approximately biweekly. In 1970 harvest plots ranged from 0.25 to 0.5 m² in size. In 1971 some

TABLE I

DISTINGUISHING CHARACTERISTICS OF THE LOCATION AND ENVIRONMENTS OF THE 10 GRASSLAND SITES
FOR WHICH NET PRIMARY PRODUCTION WAS CALCULATED

| Site | Latitude (°N) | Longitude (°W) | Annual Precipitation (mm) | | | Growing Season Precipitation (mm) | | | Average Growing Season Temp. (°C) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1970 | 1971 | 1972 | 1970 | 1971 | 1972 | 1970 | 1971 | 1972 |
| ALE | 46°24' | 119°33' | -- | 178 | 158 | -- | 89 | 109 | -- | 17.4 | 15.2 |
| Bison | 47°19' | 114°16' | 403 | -- | -- | 244 | -- | -- | 14.3 | -- | -- |
| Bridger | 45°47' | 110°47' | 984 | -- | -- | 182 | -- | -- | 12.7 | -- | 11.3 |
| Cottonwood | 43°47' | 101°52' | 415 | 676 | 409 | 242 | 485 | 354 | 18.1 | 16.4 | 13.6 |
| Dickinson | 46°54' | 102°49' | 512 | -- | -- | 360 | -- | -- | 15.8 | -- | -- |
| Hays | 38°52' | 99°23' | 461 | -- | -- | 426 | -- | -- | 18.4 | -- | -- |
| Jornada | 32°36' | 106°51' | 166 | 186 | 345 | 166 | 183 | 324 | 15.3 | 17.7 | 16.7 |
| Osage | 36°57' | 96°33' | 652 | 947 | 867 | 435 | 782 | 805 | 19.0 | 19.3 | 19.2 |
| Pantex | 35°18' | 101°32' | 243 | 592 | 390 | 184 | 522 | 359 | 17.9 | 17.5 | 17.3 |
| Pawnee | 40°49' | 104°46' | 242 | 262 | 331 | 149 | 222 | 324 | 15.5 | 14.7 | 14.8 |

sites (ALE, Jornada, and the first sampling date for Osage) used two quadrat sizes for harvesting, 0.5 m² and 2.0 m². The remaining sites employed 0.5-m² quadrats as did all sites in 1972. All aerial plant material was clipped at the soil surface and separated by species if it was standing material. The dead plant material fallen on the ground was collected as litter. Crowns were not included in this clipped material. All harvested vegetation was oven-dried at 50° to 60°C. Litter was collected variously by hand or with a vacuum cleaner in 1970 and by vacuum cleaner in 1971 and 1972. The change from hand collection to vacuum collection increased amounts of litter collected approximately by a factor of 2. Litter weights are expressed on an ash-free basis and other aerial material on a dry-weight basis.

At all sites except for Pawnee 1970 and 1971 aerial standing plant biomass was separated into live and dead components. In 1970 Cottonwood, Dickinson, Jornada, and Osage Sites further separated the dead material into old and recent dead by species. At the Bison Site in 1970 old and recent dead were separated, but not by species. In 1971 and 1972, sites, other than Pawnee 1971 and ALE 1971, also separated old (standing dead material carried over from previous years' growth) and recent dead (material produced and senesced in the current sampling season) by species. The criteria for separating old from recent dead were physical appearance and color. The recent dead material was usually light, unweathered yellow in color often attached to green portions of the shoot. The old dead was somewhat weathered and brown to dark brown in color, but still standing on the ground. These criteria are subjective; however, sampling crews on various sites had some training in distinguishing these two categories. At those sites that had species with persistent aboveground parts the live material was separated into a current and perennial component [3].

## B. Methods of Calculations

The aboveground net primary production for the growing season has been calculated by the following methods:
1.   Peak standing crop of current live material. The peak community biomass (weight of the live vegetation) is taken as an estimate of ANP.
2.   Peak standing crop of current live material plus recent dead. This method includes in the estimate of ANP the material in method 1 plus the weight of current season's growth which has senesced previous to the date of peak live biomass.
3.   Summation of peak current live weights by species. Peak biomasses of individual species are summed up, assuming that all species do not reach their peaks simultaneously.

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[3] Our purpose here is not to report original data, but the same are available in the US/IBP Grassland Biome Data Library at the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins.

*4.* Summation of peak standing crop of current live plus recent dead material by species. In this method the weight of the recent dead material for the same dates when the species attained its peak live weight is added to the latter quantity. Thus the estimate includes the material in method 3 plus the weight of current season's growth, now senesced, for each species.

*5.* Trough-peak analysis on total standing crop. In this method the positive increments in the total standing crop (current live + perennial live + recent dead + old dead + litter) were summed up over time.

*6.* Trough-peak analysis on live material. This method includes the summation of positive increments in the current live material over time. The positive differences were summed with the following statistical constraints:

  *a.* No constraint — all positive differences were summed.
  *b.* Only those increments were summed which were significant at $\alpha = 0.2$.
  *c.* Only those increments were summed which were significant at $\alpha = 0.1$.
  *d.* Only those increments were summed which were significant at $\alpha = 0.05$.

*7.* Trough-peak analysis on live plus recent dead material. In this method the positive increments in the recent dead material, if and when they coincided with the positive increments in the live material, are added to the latter. The philosophy behind this is that if both live and recent dead materials increased within the same sampling interval, obviously some new production was rapidly transferred from the live compartment to the recent dead compartment. So, the method takes into account this transfer and at the same time precludes any double addition. The positive differences were summed with the statistical constraints a to d as described for method 6.

*8.* Trough-peak analysis on live plus recent dead plus old dead material. The method is similar to method 7, but the positive increments in old dead compartment are also added to the sum of increments in live and recent dead compartments if all three compartments exhibited concurrent positive increments in a sampling interval. Statistical constraints a to d were applied as in method 6.

*9.* Trough-peak analysis on live plus recent dead plus old dead plus litter. The method is similar to method 8, but any positive increment in litter compartment, if it occurred concomitantly with positive increments in the live, recent dead, and old dead compartments, is added to the estimate of ANP. Thus if there were some fast transfers of currently produced live material to litter compartment, the same would be accounted for. The increments were summed, subject to the statistical constraints a to d as in method 6.

*10.* Summation of positive increments in the standing crop of current live material by species. This is an extension of method 3, but in this case the positive increments in the live weights of

individual species are summed to allow for situations where a species exhibits more than one peak in its growth response.

*11.* Summation of positive increments in the current live weights of individual species plus summation of concurrent positive increments in the recent dead material by species. This accounts for the transfer of currently produced live material into the recent dead compartment within a sampling interval.

*12.* Summation of positive increments in the current live material of phenologically similar species groups, viz., warm season and cool season species. Statistical constraints a to d were the same as in method 6.

*13.* Summation of positive increments in the standing crop of current live material of species grouped according to longevity, viz., annual and perennial species. Statistical constraints a to d were the same as in method 6.

## IV. RESULTS

## A. Shortgrass Prairie

*1. Pantex*

Production estimates by different techniques for the Pantex Site were quite variable between treatments and among years for the same treatments (Figure 1). The estimates ranged:

| Year | Ungrazed $(g \cdot m^{-2})$ | Grazed $(g \cdot m^{-2})$ |
|------|------------------------------|----------------------------|
| 1970 | 0 to 249 | 0 to 540 |
| 1971 | 211 to 591 | 41 to 364 |
| 1972 | 213 to 981 | 163 to 851 |

The average size of the range was larger for the grazed than the ungrazed grassland.

Five of the maximum values of ANP were arrived at by the method that considered positive increases in the litter compartment together with live and dead compartments. The minimums were distributed among three methods, 6, 12, and 13.

For a large proportion of the calculations involving total standing crop or consideration of one or more compartments (methods 6, 7, 8, and 9) increasing confidence interval width had no effect on the estimate of ANP. Most positive increments were significant at all three levels. The 1970 data were the notable exceptions to the above statement. Methods 12 and 13 also involved trough-peak analysis, but the calculations were performed on species biomasses rather than compartment biomasses and more differences were found.
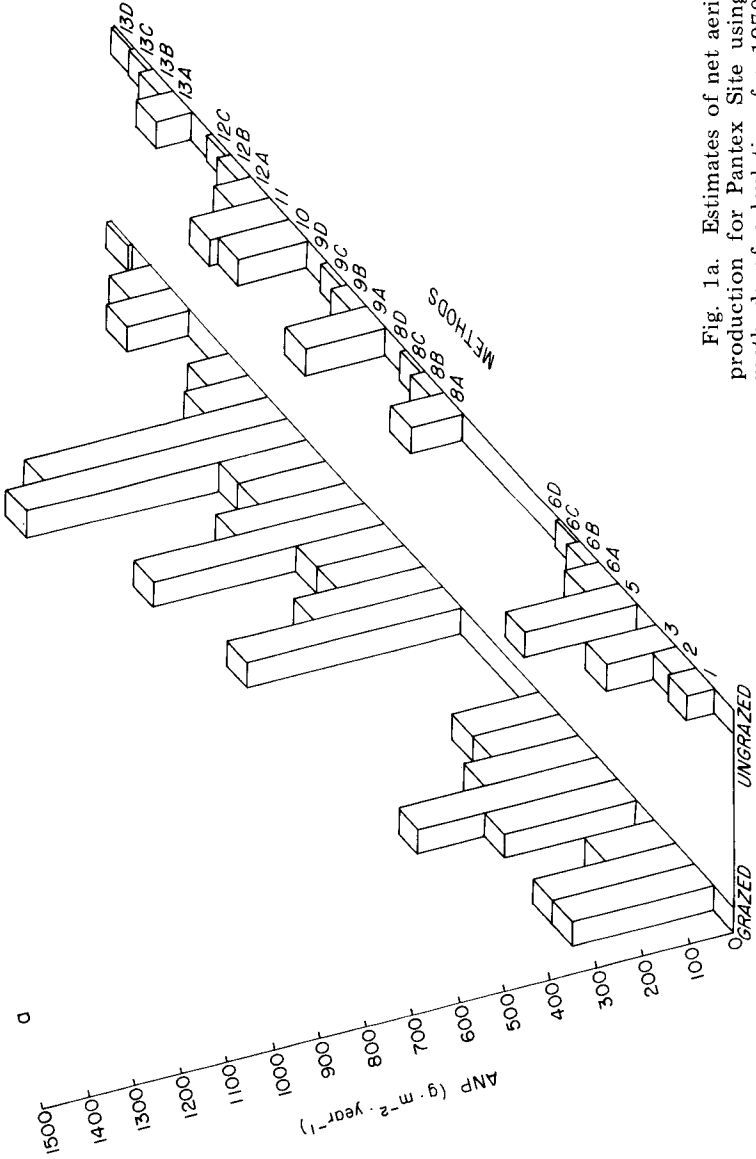
Fig. 1a. Estimates of net aerial primary production for Pantex Site using different methods of calculation for 1970. See text for explanation of numbered methods.
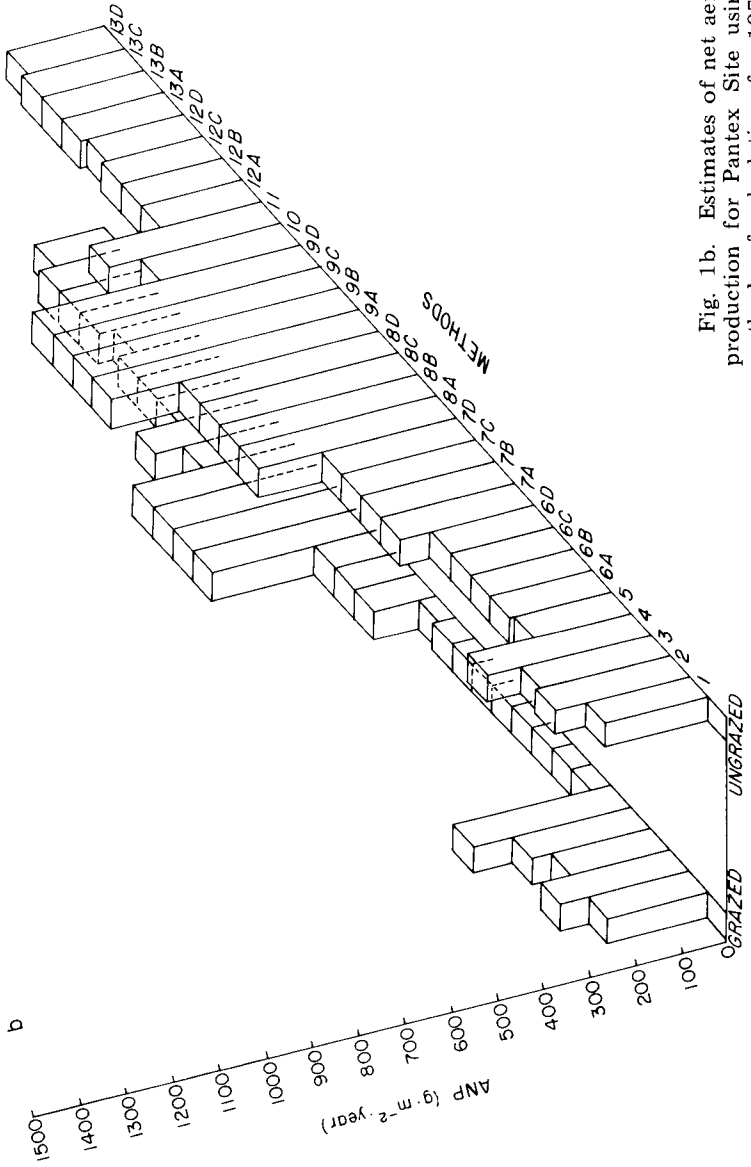
Fig. 1b. Estimates of net aerial primary production for Pantex Site using different methods of calculation for 1971. See text for explanation of numbered methods.
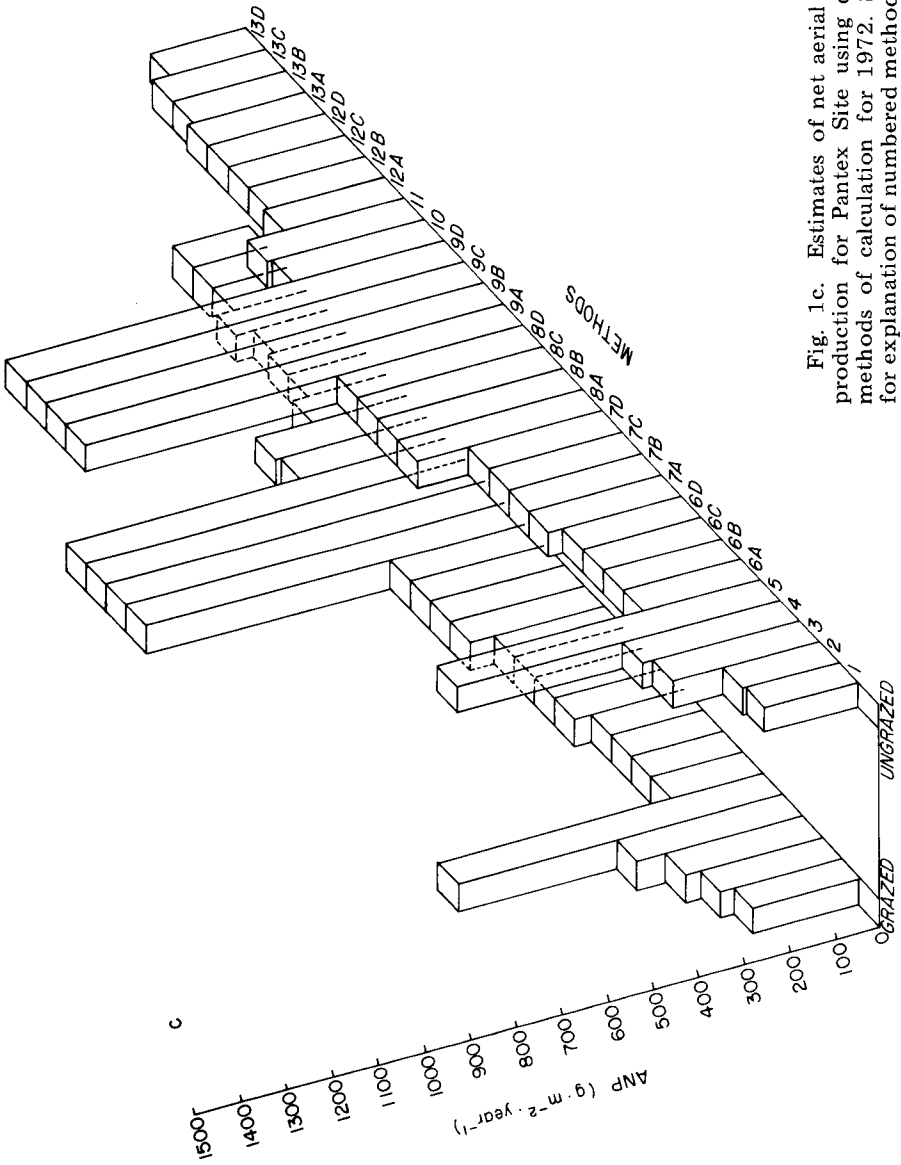
Fig. 1c. Estimates of net aerial primary production for Pantex Site using different methods of calculation for 1972. See text for explanation of numbered methods.

## 2. Pawnee

Much of the Pawnee data were not appropriate for our analyses. The range of estimates of ANP is from 204 to 63 g $\cdot$ m$^{-2}$ for the ungrazed grassland in 1972 and 289 to 32 g $\cdot$ m$^{-2}$ for the grazed grassland (Figure 2). In 1970 and 1971 only a single estimate is available for each grazing treatment.

The lowest estimates of ANP for the Pawnee data were arrived at by methods 12 and 13. Both methods involve summing positive increments of live biomass by groups of species. These values are approximately 50% of the values obtained by summing positive increments by species. The largest estimates were arrived at by methods 5 and 11.

The data for the grazed site were quite variable as indicated by methods involving statistical criteria. In all cases, there was one estimate at the zero significance level and another at the 80%, 90%, and 95% level. With the exception of method 5 in one year and methods 8 and 9, all other methods indicate that ANP was reduced by the grazing treatment.

## B. Mixed-grass Prairie

## 1. Dickinson

The estimates of ANP for the Dickinson Site ranged from 119 to 471 g $\cdot$ m$^{-2}$ for the ungrazed treatment and from 160 to 436 g $\cdot$ m$^{-2}$ for the grazed grasslands (Figure 3). Both of the maximum values (471 ungrazed and 436 grazed) were arrived at by method 11. Method 13 at the 95% significance level produced the lowest values for both treatments. The differences between the maxima and the minima for the treatments were 352 and 276 g $\cdot$ m$^{-2}$, respectively, for ungrazed and grazed treatments. The two methods most commonly seen in the literature (1 and 3) yielded estimates of 182 and 351 g $\cdot$ m$^{-2}$ for the ungrazed grasslands and 218 and 302 g $\cdot$ m$^{-2}$ for the grazed. For the ungrazed grassland the method 1 estimate was 39% of the maximum and 153% of the minimum. The method 1 estimate for the grazed grassland was 50% of the maximum and 136% of the minimum. Method 3 yielded estimates closer to the maxima for both treatments.

Method 9 included summation of the concurrent positive increments in live, recent dead, old dead, and litter, and the estimates arrived at by this method employing four significance level criteria indicate that all of the concurrent increments in biomass of the above mentioned compartments were based on significantly different biomass estimates. If this is in reality the most valid estimate of ANP, then in the case of the ungrazed grassland the majority of the methods including 1 and 3 underestimate ANP. In the case of the grazed grassland the four significance levels result in three different estimates of ANP. If the 95% level of significance is accepted as the standard, most of the methods overestimate ANP. If the 90% or 80% level of confidence is acceptable, the estimates are very close to the mean of all methods.
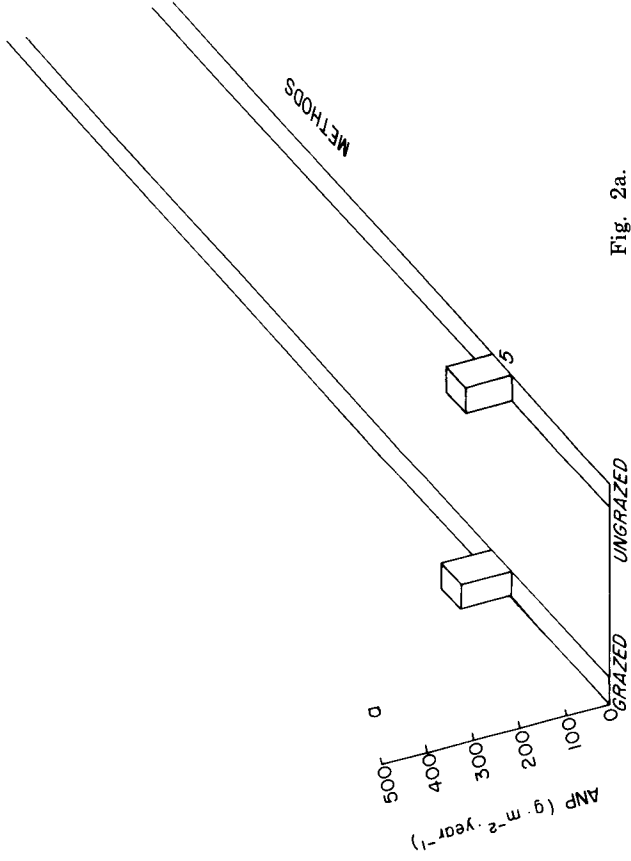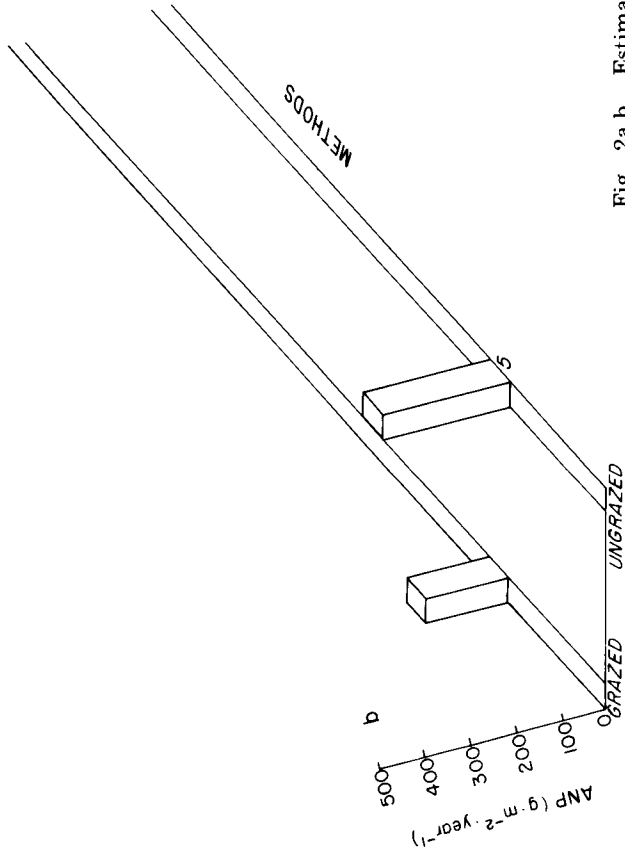
Fig. 2a.

Fig. 2a,b. Estimates of net aerial primary production for Pawnee Site using different methods of calculation for 1970, and 1971. See text for explanation of numbered methods.
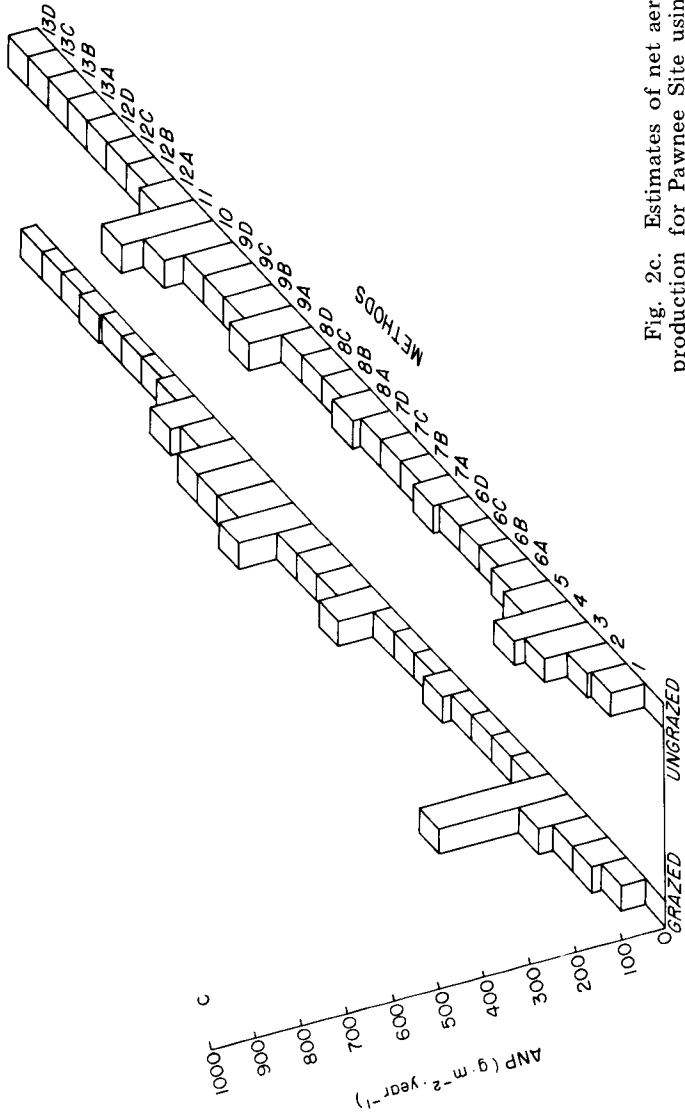
Fig. 2c. Estimates of net aerial primary production for Pawnee Site using different methods of calculation for 1972. See text for explanation of numbered methods.
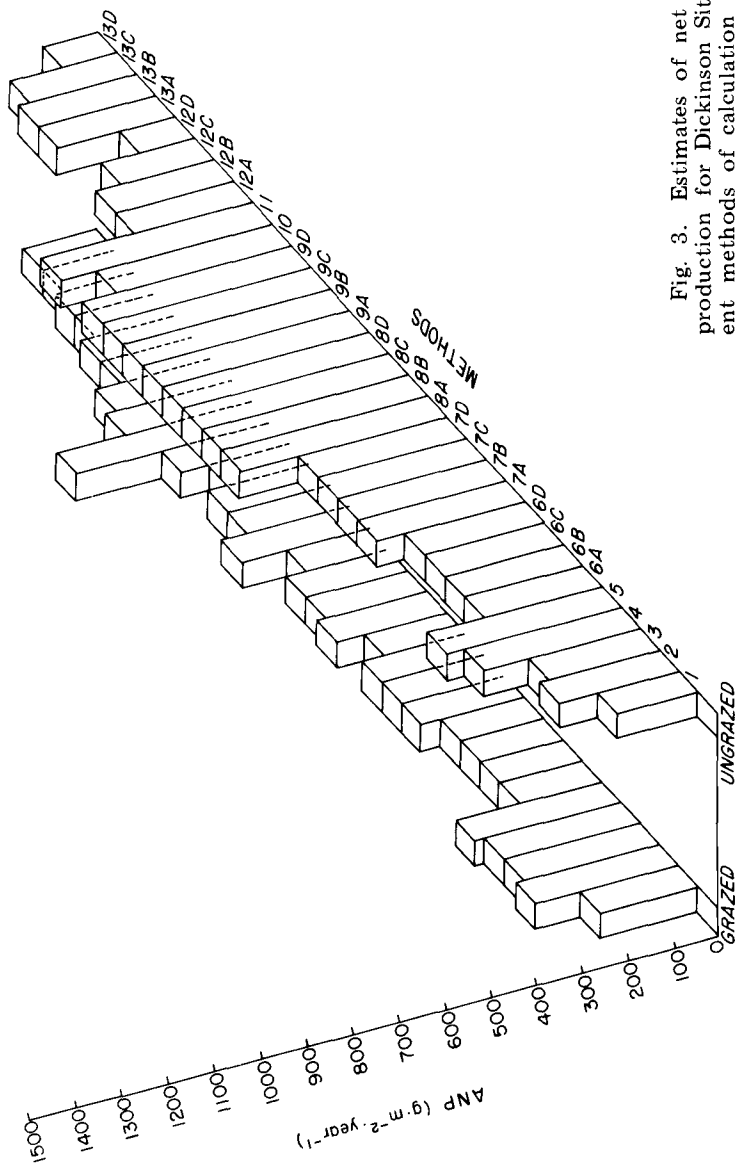
Fig. 3. Estimates of net aerial primary production for Dickinson Site using different methods of calculation for 1970. See text for explanation of numbered methods.
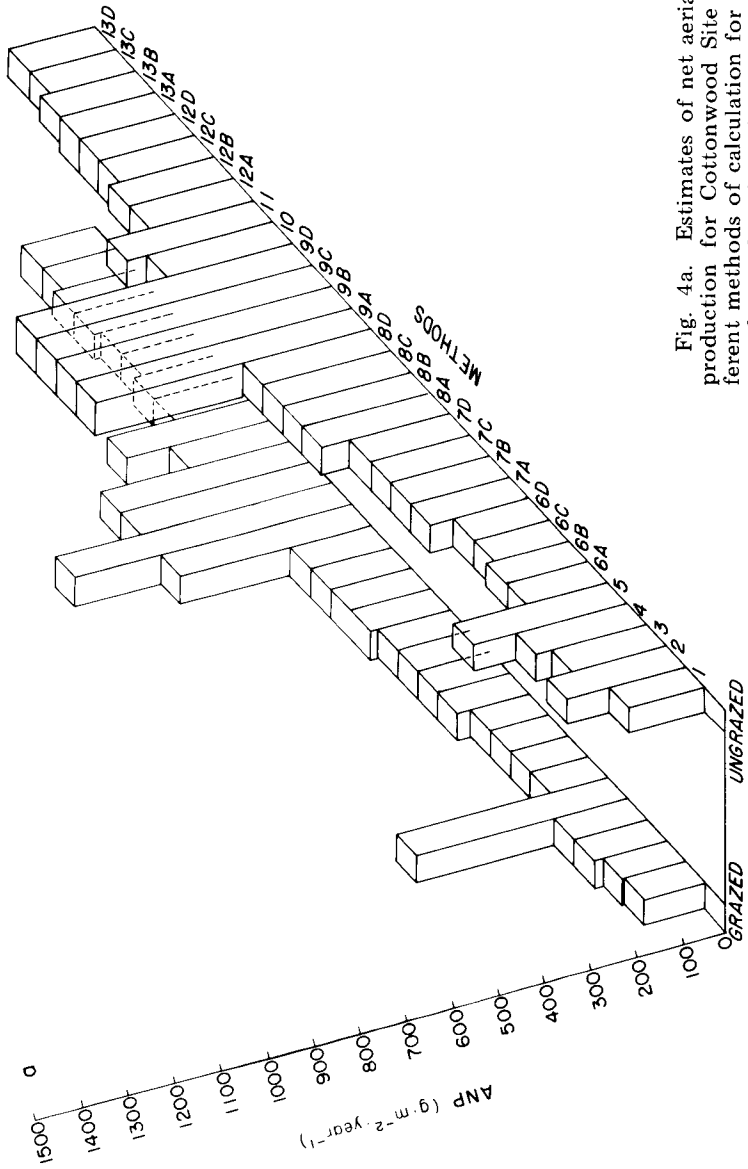
Fig. 4a. Estimates of net aerial primary production for Cottonwood Site using different methods of calculation for 1970. See text for explanation of numbered methods.

Fig. 4b. Estimates of net aerial primary production for Cottonwood Site using different methods of calculation for 1971. See text for explanation of numbered methods.
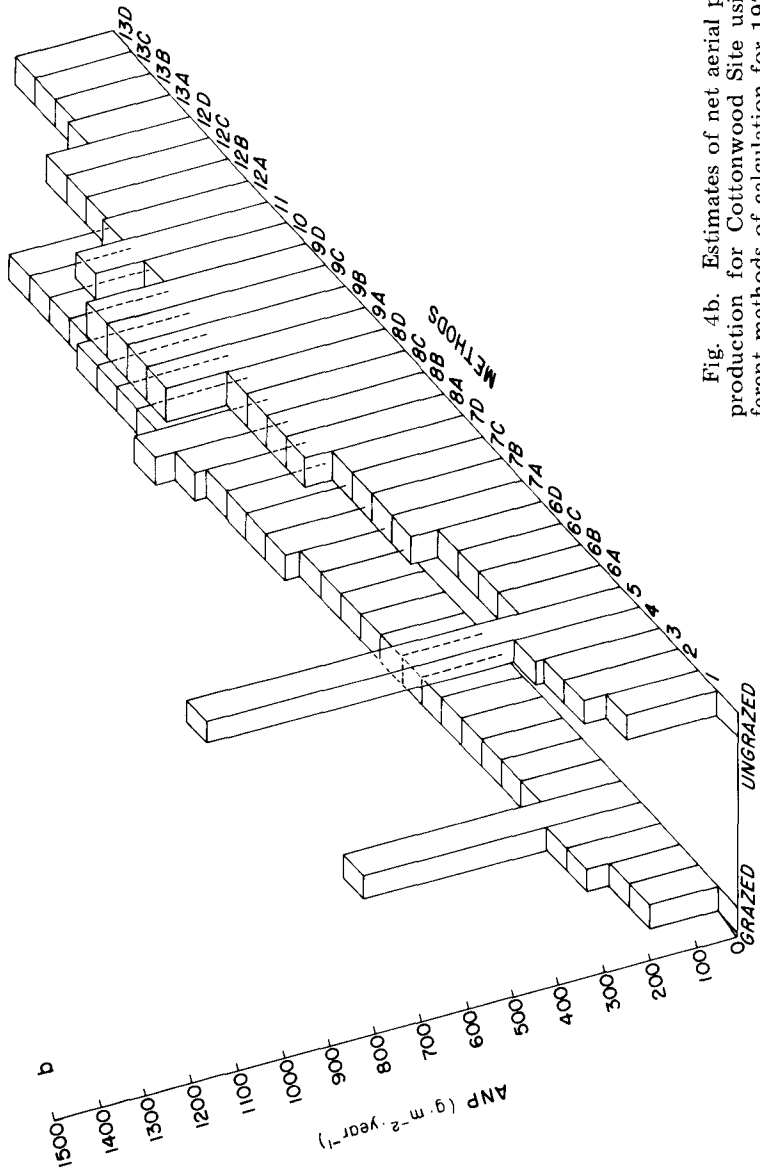
Fig. 4c. Estimates of net aerial primary production for Cottonwood Site using different methods of calculation for 1972. See text for explanation of numbered methods.

Fig. 5. Estimates of net aerial primary production for Hays Site using different methods of calculation for 1970. See text for explanation of numbered methods.

Fig. 6a. Estimates of net aerial primary production for Osage Site using different methods of calculation for 1970. See text for explanation of numbered methods.

Fig. 6b. Estimates of net aerial primary production for Osage Site using different methods of calculation for 1971. See text for explanation of numbered methods.

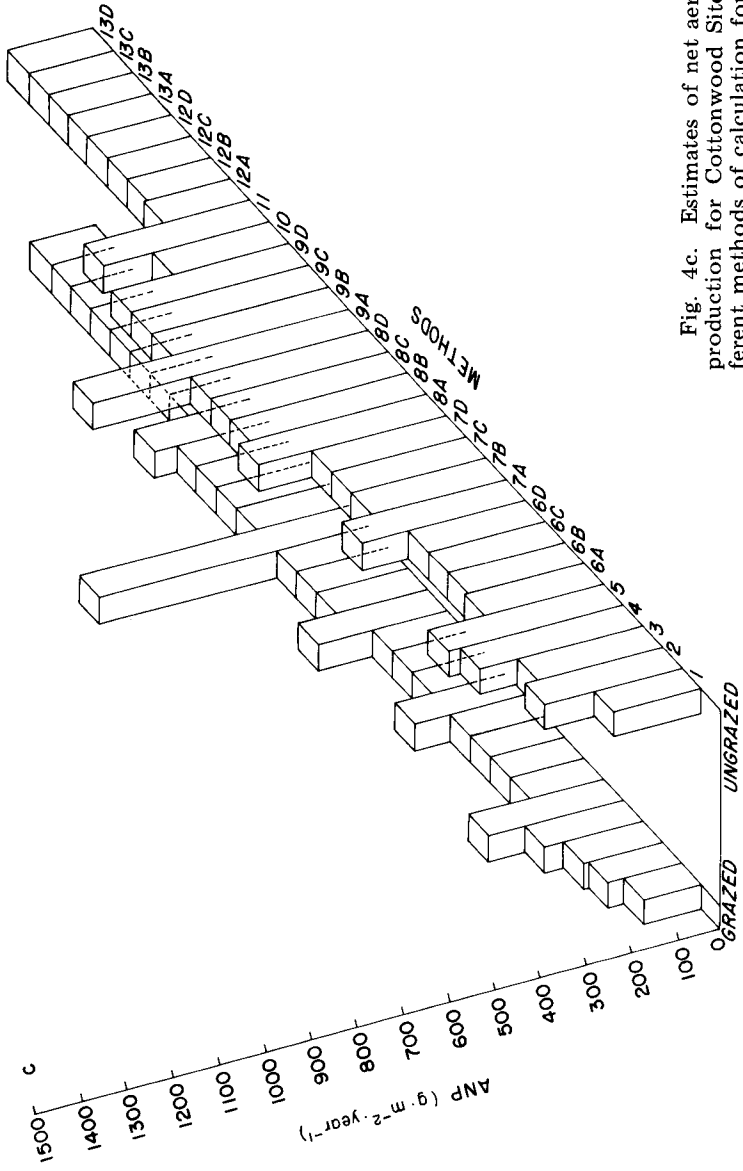Fig. 6c. Estimates of net aerial primary production for Osage Site using different methods of calculation for 1972. See text for explanation of numbered methods.
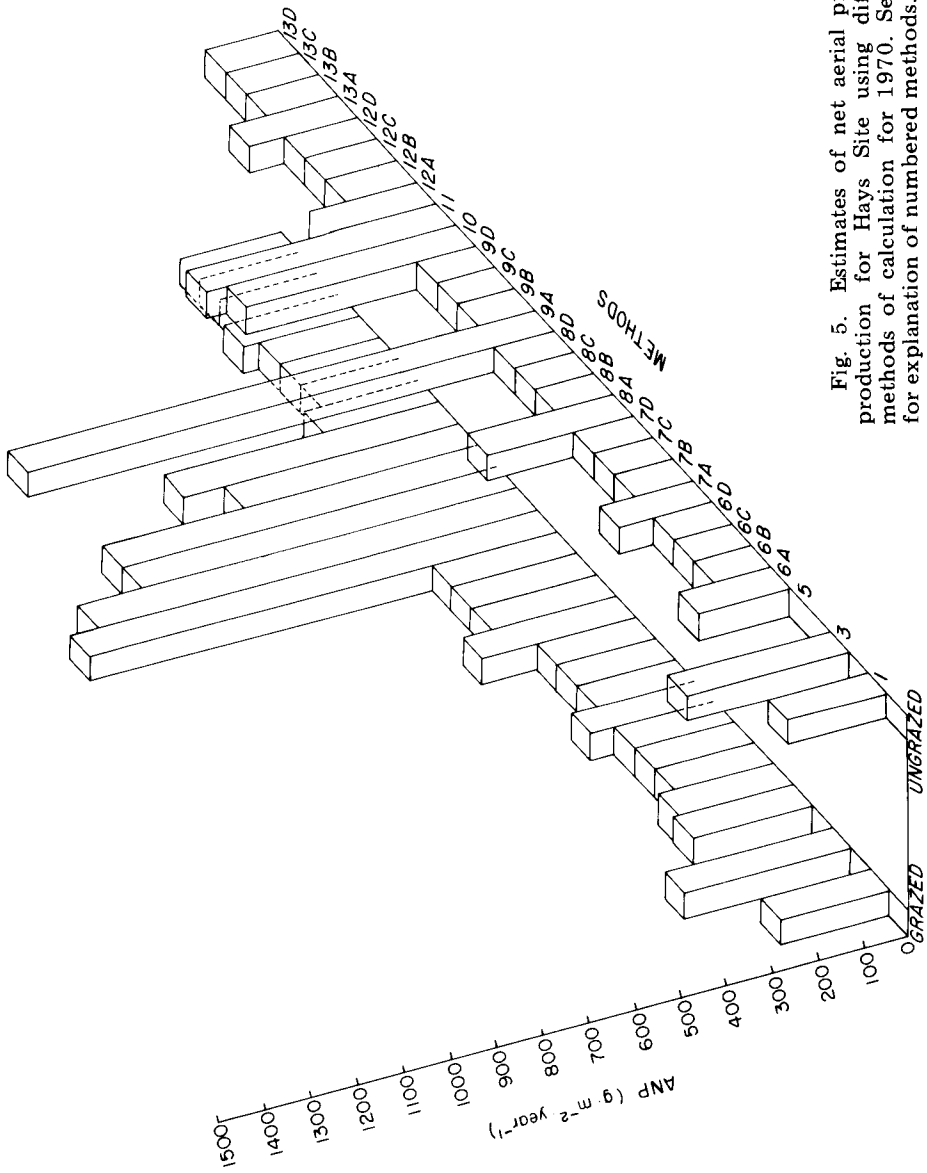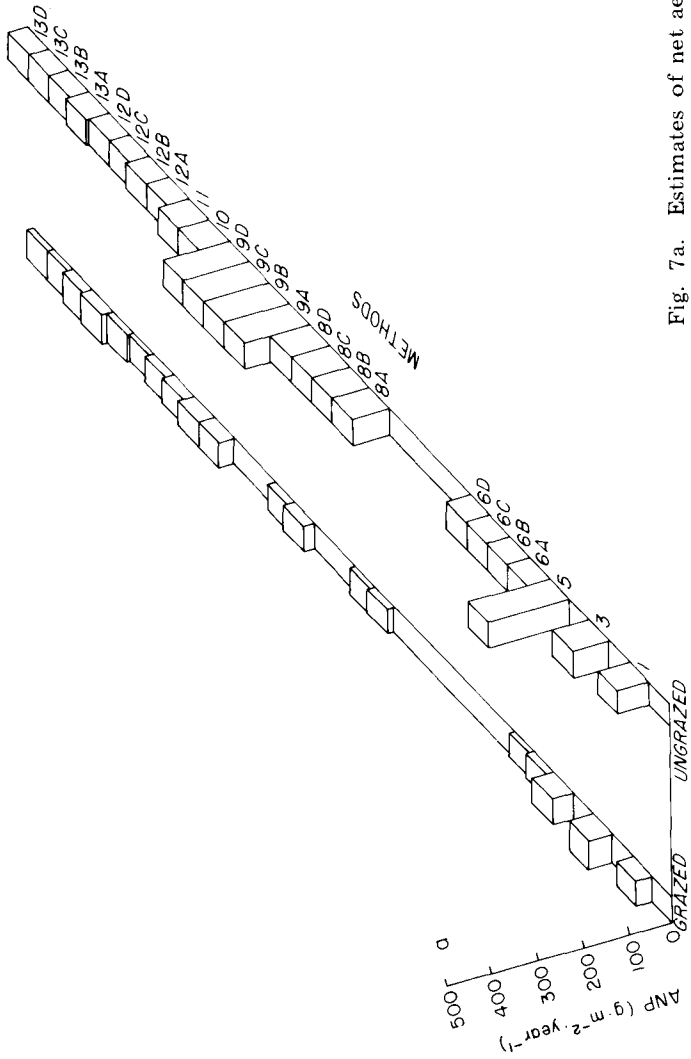
Fig. 7a. Estimates of net aerial primary production for ALE Site using different methods of calculation for 1971. See text for explanation of numbered methods.
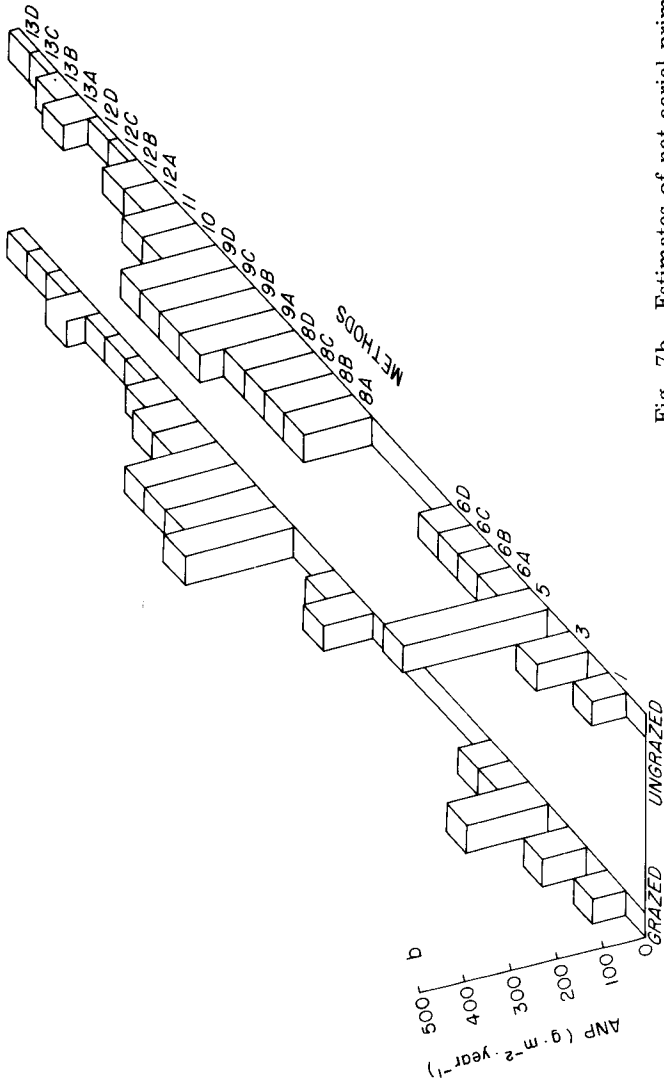
Fig. 7b.  Estimates of net aerial primary production for ALE Site using different methods of calculation for 1972. See text for explanation of numbered methods.
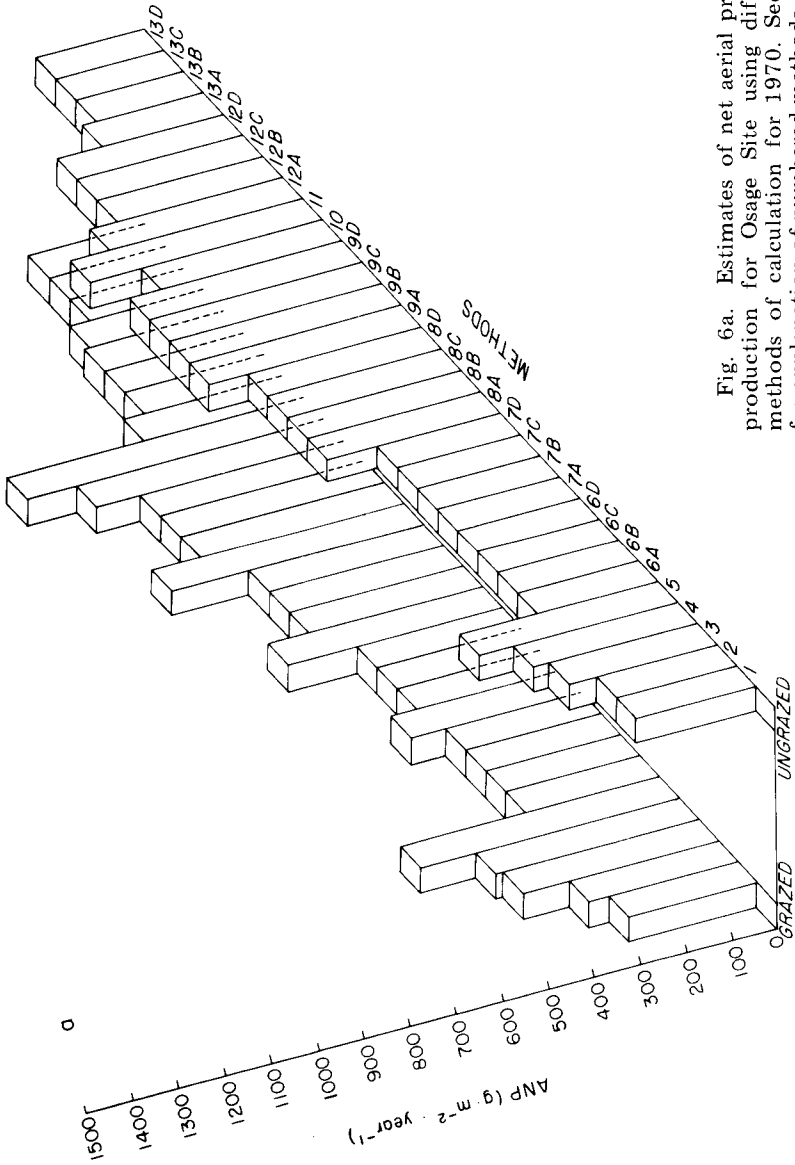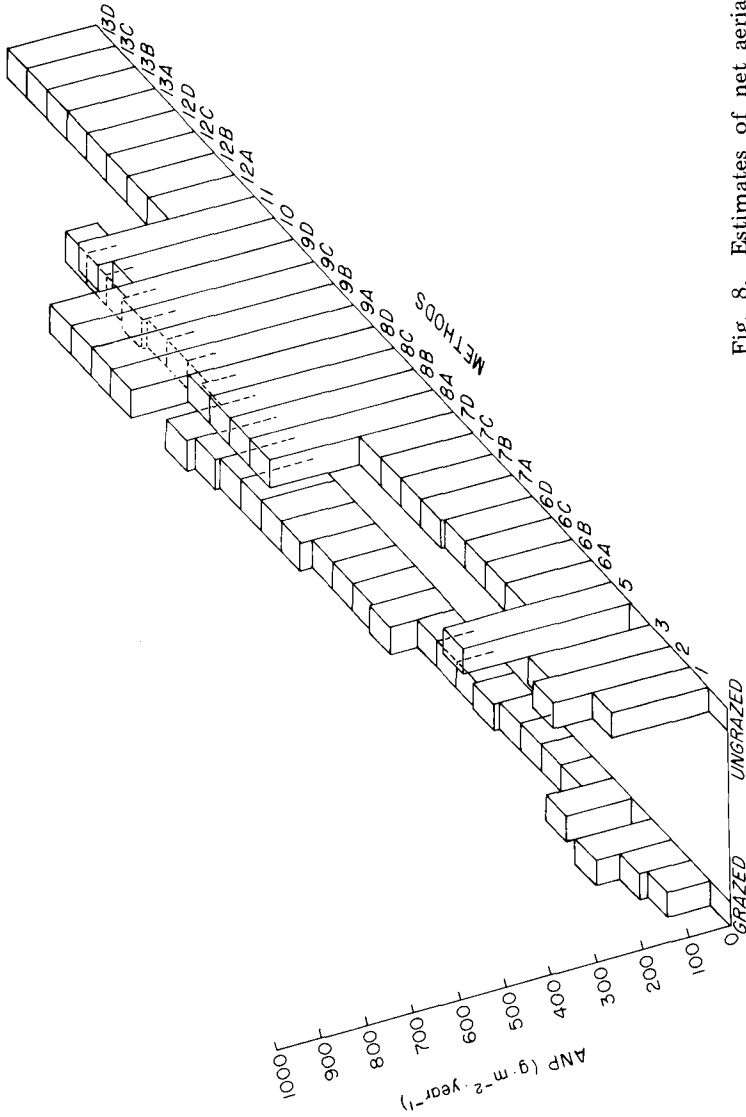
Fig. 8. Estimates of net aerial primary production for Bison Site using different methods of calculation for 1970. See text for explanation of numbered methods.
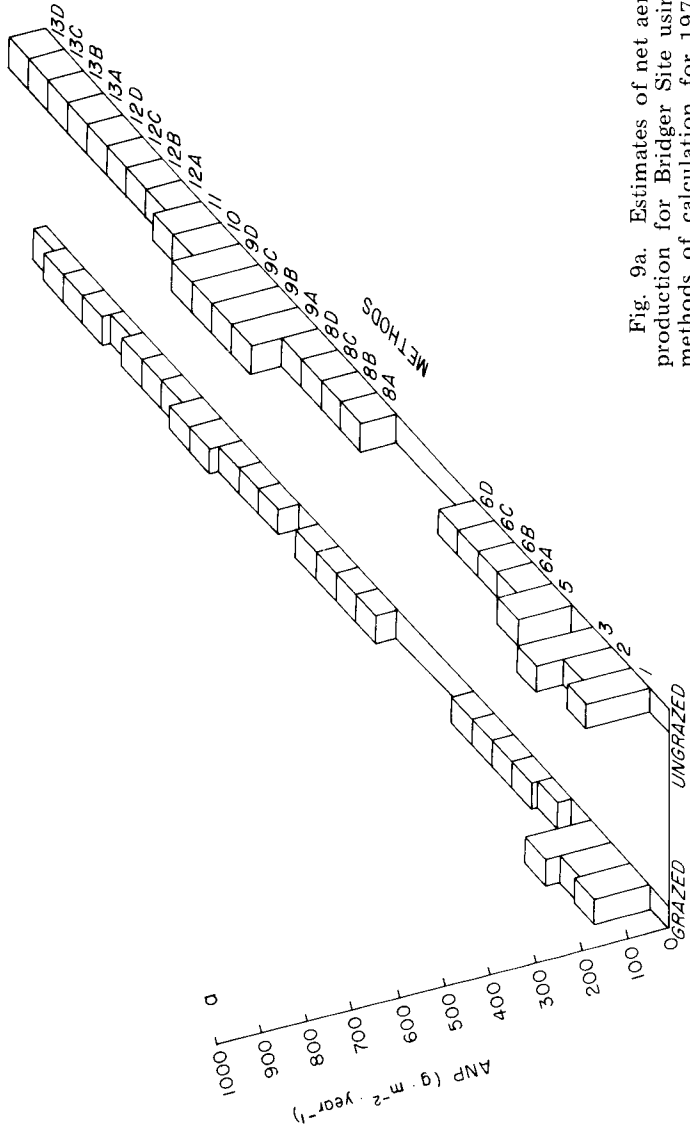
Fig. 9a. Estimates of net aerial primary production for Bridger Site using different methods of calculation for 1970. See text for explanation of numbered methods.
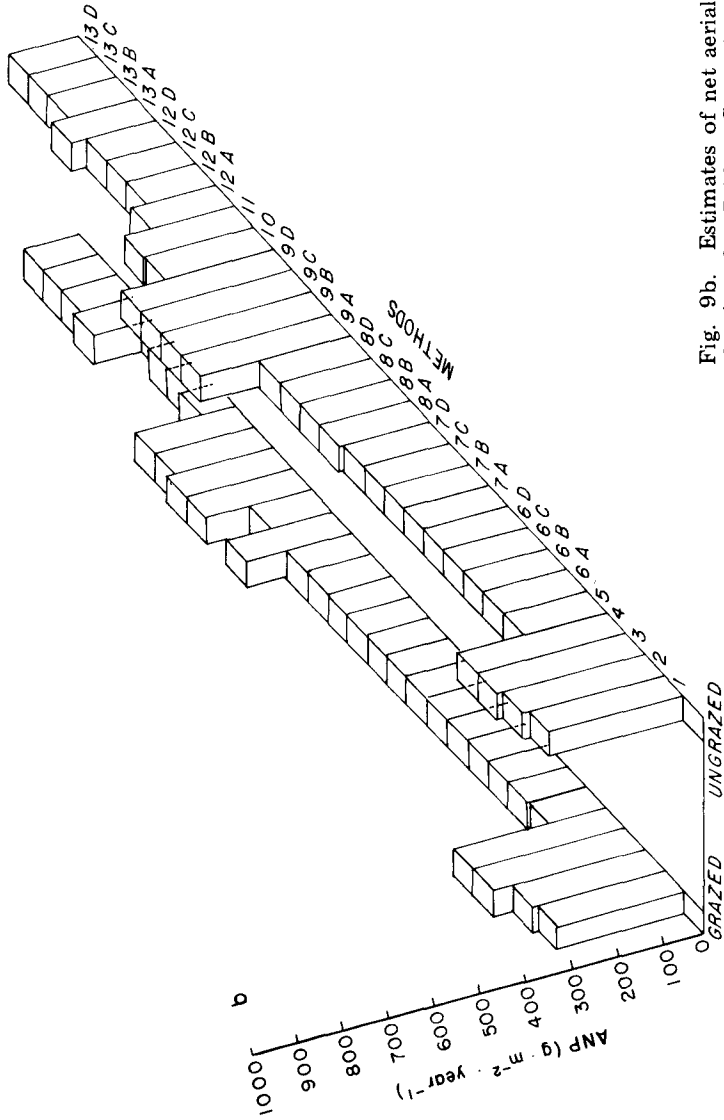
Fig. 9b. Estimates of net aerial primary production for Bridger Site using different methods of calculation for 1972. See text for explanation of numbered methods.

Fig. 10a. Estimates of net aerial primary production for Jornada Site using different methods of calculation for 1970. See text for explanation of numbered methods.
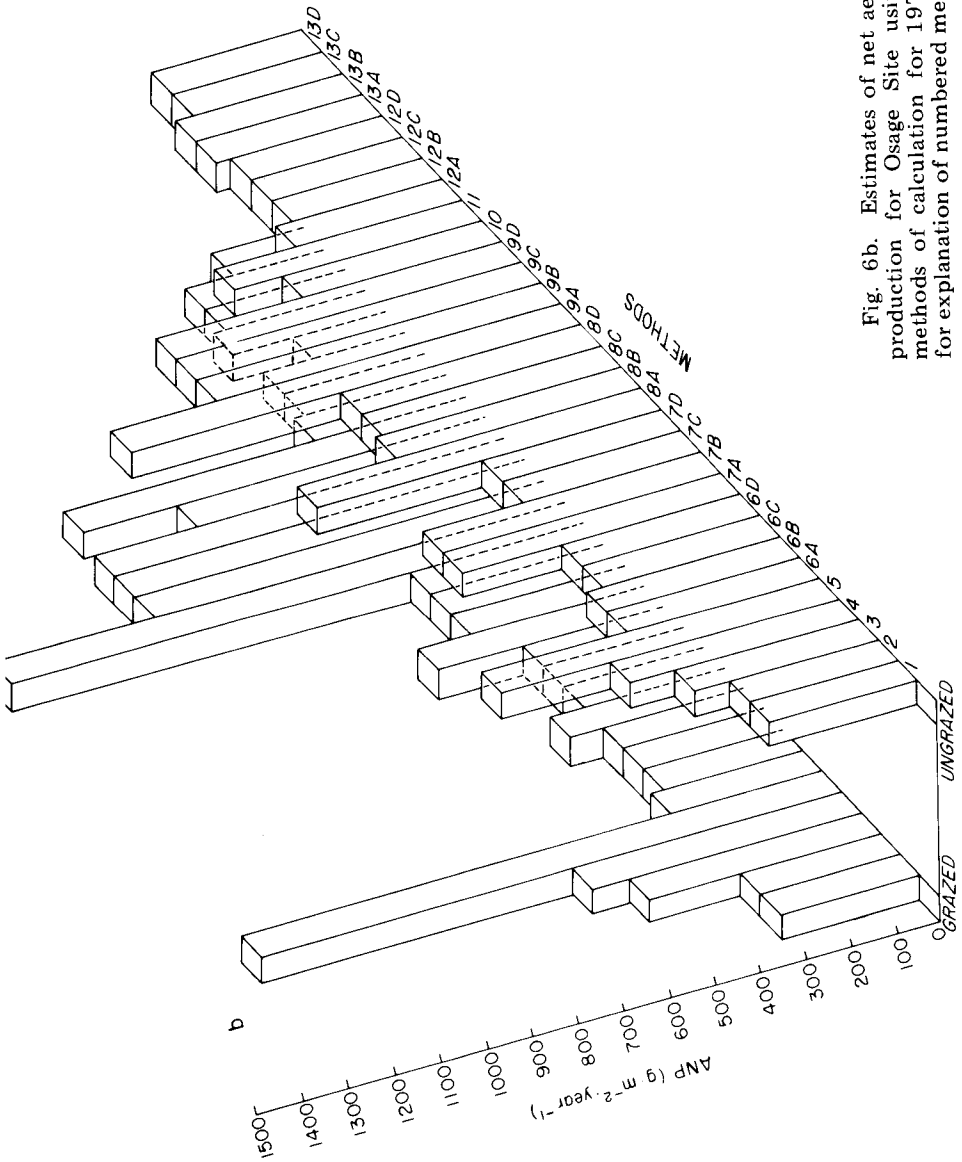
Fig. 10b. Estimates of net aerial primary production for Jornada Site using different methods of calculation for 1971. See text for explanation of numbered methods.
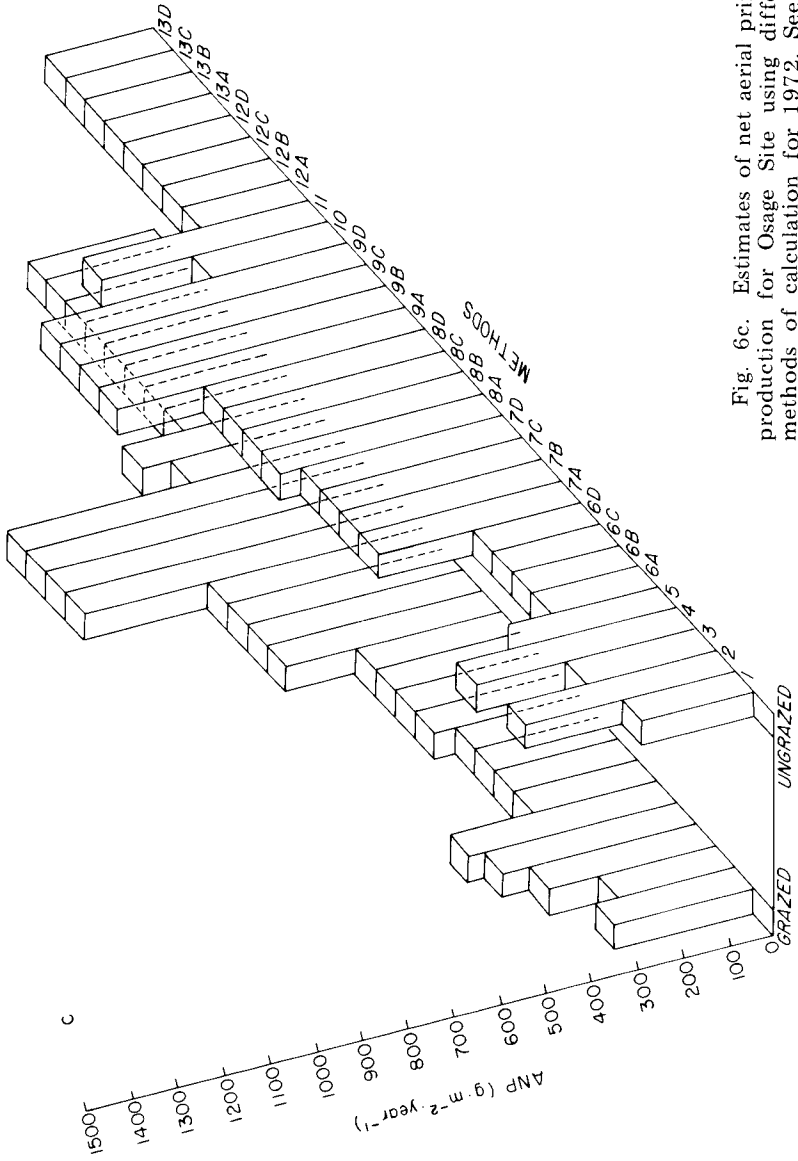
Fig. 10c. Estimates of net aerial primary production for Jornada Site using different methods of calculation for 1972. See text for explanation of numbered methods.
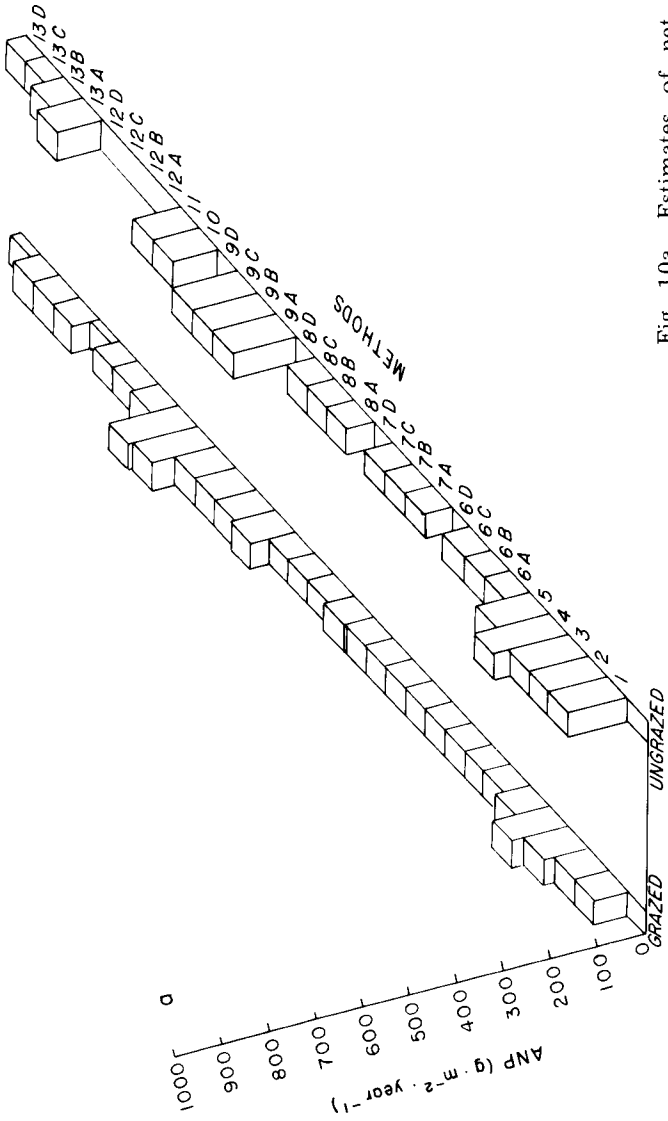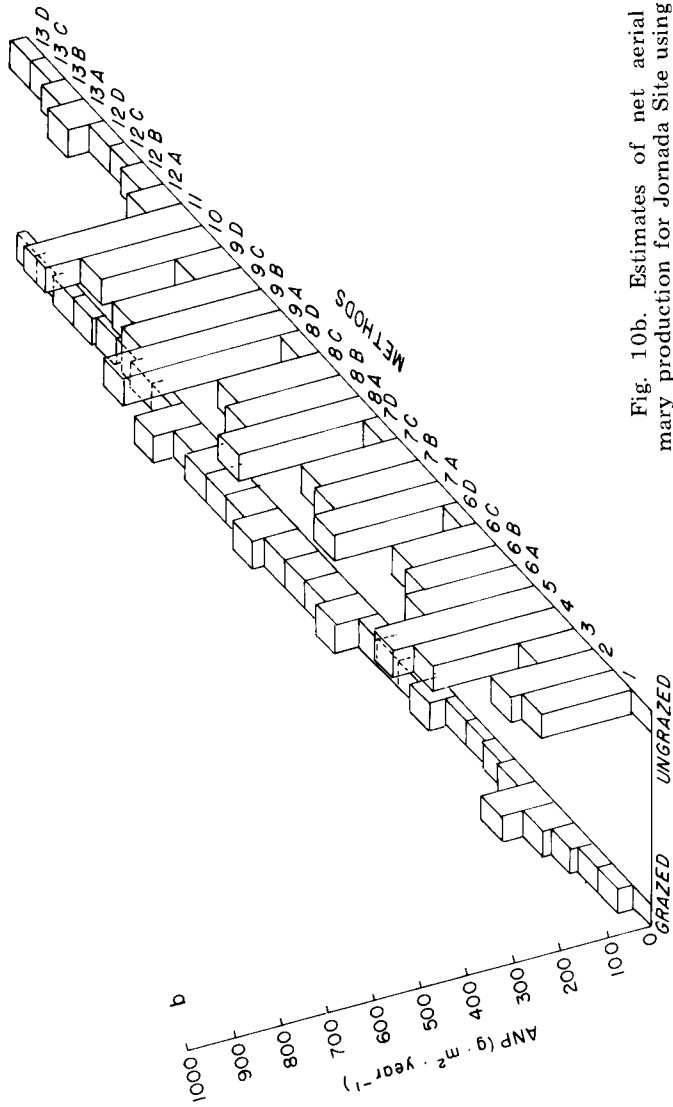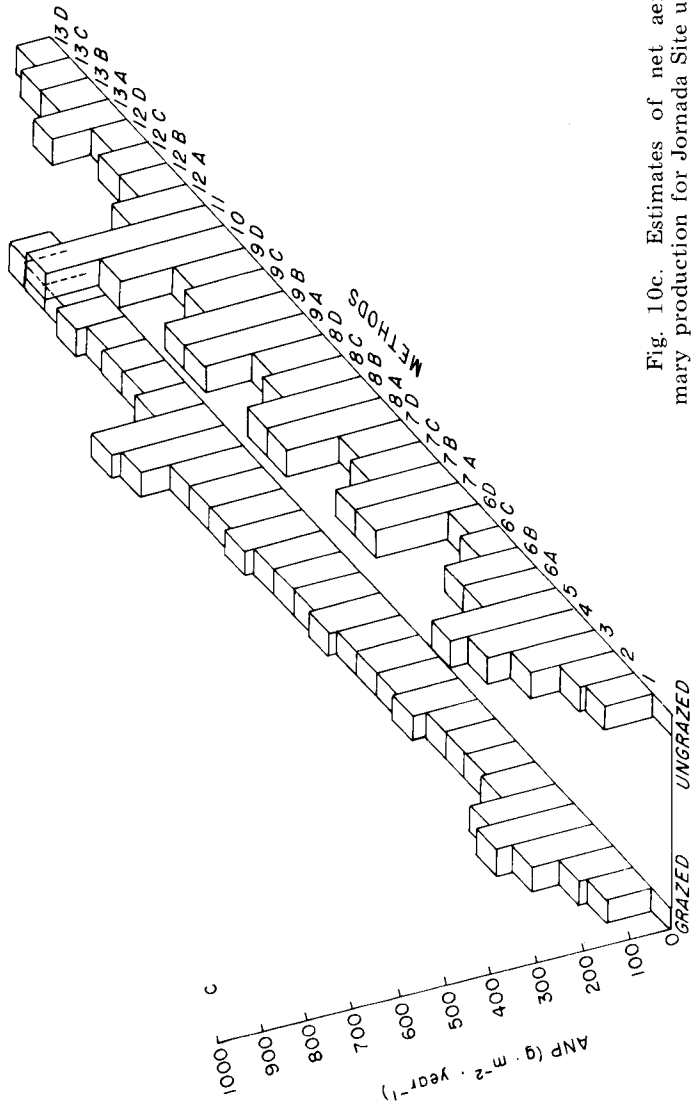
*2. Cottonwood*

The ranges of ANP were (Figure 4):

| Year | Ungrazed $(g \cdot m^{-2})$ | Grazed $(g \cdot m^{-2})$ |
|------|------------------|------------------|
| 1970 | 188 to 618 | 129 to 605 |
| 1971 | 205 to 973 | 153 to 619 |
| 1972 | 173 to 698 | 139 to 478 |

The maxima for the ungrazed treatment in 1970 and 1972 were arrived at by method 9 with the level of significance at zero. The same method accounted for the maximum in the grazed grassland in 1972. The maxima for the grazed treatment in 1970 and 1971 and the ungrazed in 1971 were calculated by method 5. Since methods 5 and 9 are the only ones which include the litter compartment in calculations, the indication is that consideration of the litter compartment accounted for a large amount in these maxima. The minimum values for all treatments and all 3 years except the ungrazed grassland in 1972 were arrived at by method 1, and for the one exception, there was a difference of only 8 $g \cdot m^{-2}$ between the estimate by method 1 and the minimum (188 $g \cdot m^{-2}$) yielded by methods 12 and 13. The fact that the community peak live biomass as an estimator of ANP always yields the minimum estimate indicates that the phenologies of the important species are not similar. This is further supported by the fact that the results of method 3 are greater than those of method 1.

On the average, the size of the range (maximum to minimum) was smaller for the ungrazed grassland than for the grazed. This differs from the other mixed prairie sites where the ranges were smaller for the grazed grassland and refers perhaps to the differences in the sampling precision.

Increasing the width of the confidence interval in the trough-peak analysis (methods 6, 7, 8, 9, 12, and 13) had approximately the same effect regardless of treatment. In many cases increasing the significance level had no effect on the estimate of ANP. In other cases two or three different values resulted.

*3. Hays*

Hays was the southern-most mixed prairie site, and ANP estimates for the ungrazed grasslands ranged from a low of 128 $g \cdot m^{-2}$ to a high of 2678 $g \cdot m^{-2}$ (Figure 5). The maximum value was obtained by method 5 and a large proportion of the production was contributed by litter. A very high amount of litter and high variability in its sampling gives little credence to this method on this site. The next maximum for comparison purposes is 557 $g \cdot m^{-2}$, arrived at by

method 11. For the grazed grassland, method 9a yielded the maximum value of 1036 g $\cdot$ m$^{-2}$. Without this value, however, the range was from 216 to 609 g $\cdot$ m$^{-2}$. The estimates of ANP by all but two of the methods for the grazed treatment were greater than for the ungrazed treatment.

Summation of peak live biomass by species (method 3) increased the estimate of ANP by 35% over the community peak live biomass for the ungrazed grassland and was only 65% of the maximum estimate. For the grazed grassland method 3 increased the estimate by 35% over method 1, but was only 39% of the maximum.

The distribution of total biomass of the various compartments (live, recent dead, old dead, and litter) as well as species biomass was apparently more uniform over the area of the grazed treatment than the ungrazed. This statement is supported by the results of the trough-peak analysis with variable significance level criteria. In all cases, even with only an 80% significance level requirement, the estimate of ANP for the ungrazed grassland was drastically reduced. The same values for the grazed grassland were also reduced by increasing the significance level but not as drastically.

## C. Tallgrass Prairie

### 1. Osage

Net productivity in this tallgrass prairie (Figure 6) as estimated by different techniques varies:

|  | Ungrazed | Grazed |
|---|---|---|
| Year | (g $\cdot$ m$^{-2}$) | (g $\cdot$ m$^{-2}$) |
| 1970 | 240 to 516 | 256 to 660 |
| 1971 | 335 to 1010 | 204 to 1309 |
| 1972 | 239 to 686 | 276 to 762 |

Method 13d consistently yielded the minimum estimate while the maximum estimate was obtained either by method 9a (thrice) or 5 (once) or method 11 (twice).

If three different investigators applied three different techniques for estimating net production on this site, they are likely to arrive at different conclusions regarding the response of net production to grazing. The investigator using method 2 (peak standing crop) as the criterion of production would find decreased production in the grazed treatment compared to ungrazed treatment for 1971 and 1972 and increased production for 1970. However, the differences in the production estimates of the two treatments are so small that one is likely to conclude that grazing till recent past has no effect on the productivity of the grassland or at best the response to grazing is erratic. On the other hand, the investigator using method 3 (sum of peak live weights of species) would consistently find a substantial

increase in net production in the grazed treatment, concluding that grazing stimulates net aboveground production. In contrast to the above two findings, the investigator using methods 8b, c, d would consistently estimate lower net production in the grazed treatment. Thus, of 31 computational schemes, four consistently yield higher estimates for the grazed treatment and three yield higher estimates for the ungrazed treatment. The remaining methods estimate higher production for the ungrazed treatment for some years and for the grazed treatment for other years.

Application of trough-peak analysis where different levels of confidences (from $\alpha > 0.2$ to $\alpha < 0.05$) are used in summing up the positive differences indicate similar results in 1972. In 1970 and1971, however, the summation of differences with $\alpha < 0.2, \alpha > 0.1$, or $\alpha < 0.05$ yields a somewhat lower estimate than the estimate obtained without any statistical constraint. This may indicate greater sampling precision in 1972. Successive concurrent additions of recent dead, old dead, and litter compartments to the live compartment while applying trough-peak analysis increases the estimate successively. The trough- peak analysis on individual species results in higher estimates than when the species are grouped either on the basis of seasonal response (cool and warm season species) or longevity (annual and perennial).

## D. Northwest Bunchgrass

### 1. ALE
On this site since recent dead was not separated from old dead, methods 2, 4, and 7 could not be applied. From the remaining methods, the range of production estimates (Figure 7) were:

| Year | Ungrazed $(g \cdot m^{-2})$ | Grazed $(g \cdot m^{-2})$ |
|------|------|------|
| 1971 | 44 to 183 | 0 to 54 |
| 1972 | 20 to 326 | 0 to 244 |

In both years method 5 yielded the highest estimate for the ungrazed treatment while in the grazed treatment the highest estimates were obtained by method 9a in 1972 and method 3 in 1971. In 1971 all the methods yielded lower estimates for the grazed treatment; while in 1972 methods 9a, 12c, 12d, 13c, and 13d yielded greater estimates for the grazed treatment, the remaining methods showed higher production on the ungrazed treatment. In both years putting statistical constraints on the positive differences in the trough-peak analysis (methods 6, 8, and 9) did not alter the results in the ungrazed treatment. On the other hand, there was a substantial decrease in the estimate of production by increasing the constraint from $\alpha > 0.2$ to $\alpha < 0.05$ in the grazed treatment. Perhaps the sampling procedure was more precise for the ungrazed treatment as compared to the grazed treatment.

*2. Bison*

The estimates of net aboveground production on this site range from 194 to 541 g · m⁻² in the ungrazed treatment and 63 to 197 g·m⁻² in the grazed treatment (Figure 8). All the methods consistently gave lower estimates for the grazed treatment. There was no effect of statistical constraints on the trough-peak analysis in the ungrazed site, but on the grazed site the constraints resulted in slightly lower estimates, though the differences are not marked. As in other cases, consideration of more than one compartment in the trough-peak analysis increased the estimate from 194 (live compartment alone) to 541 g · m⁻² (live, dead, and litter compartments) in ungrazed and from 75 to 168 g · m⁻² in the grazed grassland. In the ungrazed treatment the highest estimate was obtained by methods 9a, b, c, d while in the grazed grassland the same was obtained by method 11. It is interesting to note that the greatest estimate for the grazed site is only 27 g · m⁻² higher than method 3 while in the ungrazed treatment the highest estimate is 269 g · m⁻² greater. Also, method 3 in the ungrazed treatment gave a lower estimate as compared to the peak standing crop (method 2), but on the grazed treatment the same yielded a higher estimate as compared to peak standing crop value.

## E. High-mountain Grassland

*1. Bridger*

The estimates of production for this site ranged:

| Year | Ungrazed $(g \cdot m^{-2})$ | Grazed $(g \cdot m^{-2})$ |
|------|------------------------------|----------------------------|
| 1970 | 81 to 168 | 27 to 145 |
| 1972 | 153 to 340 | 58 to 344 |

For both treatments in 1970 the highest and lowest estimates were provided by the same methods, while in 1972 different methods provided the highest and lowest estimates for different treatments (Figure 9). Also in 1970 all the methods estimated lower production on the grazed site; while in 1972 methods 3 and 4 estimated slightly higher production on the grazed site, the rest of the methods estimated higher production for the ungrazed site. Sum of the peak live biomass by species yielded the highest estimates for three out of four data sets and for the remaining one its estimate was only 10 g · m⁻² lower than the highest estimate. Estimates from methods 6, 7, and 8 were low. However, sampling on this site started on 30 June 1970 and 12 June 1972. By this time apparently considerable growth had taken place, live biomass on first sampling dates were 63 (ungrazed) and 78 g · m⁻² (grazed) in 1970 and 115 (ungrazed) and 151 g · m⁻² (grazed) in 1972. These amounts should be added to the estimates from trough-peak analysis for estimating ANP for the whole growing season.

## F. Desert Grassland

### 1. Jornada

The estimates of production (ANP) (Figure 10) were:

| Year | Ungrazed $(g \cdot m^{-2})$ | Grazed $(g \cdot m^{-2})$ |
|------|----------|--------|
| 1970 | 0 to 172 | 19 to 151 |
| 1971 | 32 to 395 | 14 to 121 |
| 1972 | 65 to 600 | 86 to 251 |

The minimum and maximum estimates are obtained by different methods in different years and in different treatments. If one were comparing the productivity of this grassland in different years and in different treatments, he will get a different picture depending upon the method used to estimate production. This is illustrated by the following example--where various treatments/years are ordered according to decreasing productivity.

(1)  On the basis of method(s) yielding minimum estimate:
     1972 grazed > 1972 ungrazed > 1971 ungrazed > 1970 grazed > 1971 grazed > 1970 ungrazed.
(2)  On the basis of of method(s) yielding maximum estimate:
     1972 ungrazed > 1971 ungrazed > 1972 grazed > 1970 ungrazed > 1970 grazed > 1971 grazed.
(3)  On the basis of of method 3:
     1972 ungrazed > 1972 grazed > 1970 ungrazed > 1971 ungrazed > 1970 grazed > 1971 grazed.
(4)  On the basis of methods 1 or 2:
     1971 ungrazed > 1970 ungrazed > 1972 ungrazed > 1972 grazed > 1970 grazed > 1971 grazed.

The application of trough-peak analysis (methods 6, 7, 8, 9) as an estimator of net production illustrates two important points. First, simultaneous consideration of more than one compartment (compare estimates from methods 6a, b,c,d with 7a, b, c, d; 7a, b, c, d with 8a, b, c, d; and 8a, b, c, d with 9a, b, c, d) results in higher estimates of production. Secondly, increasing the rigidity of the statistical constraints ($\alpha > 0.2$ to $\alpha < 0.05$) decreases the estimate of production However, this decrease in the estimated value due to increasing constraint is unequal. For example, in the ungrazed treatment in 1972 method 7a ($\alpha > 0.2$) yields an estimate of 144 $g \cdot m^{-2}$ while method 7d ($\alpha < 0.05$) yields 138 $g \cdot m^{-2}$, that is only 6 $g \cdot m^{-2}$ less. But in the ungrazed treatment of 1971 the method 7a yields 277 $g \cdot$

$m^{-2}$ while method 7d yields only $32 \; g \cdot m^{-2}$, a difference of $245 \; g \cdot m^{-2}$. This perhaps illustrates the variability in the sampling precision.

When trough-peak analysis is applied to individual species or species groups (methods 10 to 13), the grouping of species into warm and cool season components or into annual and perennial form results in a lower estimate than when individual species are considered. Method 11 yields the maximum estimate 50% of the time.

## V. DISCUSSION

In the foregoing section we have shown that wide differences in the estimate of production can result by using different techniques of calculation on the same data set or the same technique on different data sets. It is also apparent that methods that yield minimum or maximum estimates differ from site to site. Most often, however, methods 9, 10, and 11 yield the highest estimates, and methods 1, 12, and 13 yield the minimum estimates. In this section we will attempt to answer other questions through a cross-site analysis of the estimates.

Relationships among the methods were investigated by a hierarchical clustering (Johnson, 1967) of the 31 × 31 simple correlation matrix (Figure 11). The results of this analysis indicate that all methods except 5 were significantly correlated ($r \geqslant 0.61, \alpha \leqslant 0.01$). Five basic clusters were identified:

A.    Method 5
B.    Method 9
C.    Methods 1, 2, 3, 4, 10, 11
D.    Methods 6, 7, 8
E.    Methods 12, 13

Clearly method 5 yields the most dissimilar results ($r \geqslant 0.21$ with other methods). This method involves trough-peak analysis on total standing crop, and the dissimilar results are likely a reflection of the large variability associated with litter biomass estimates.

The largest cluster includes methods 6, 7, and 8 with statistical constraints on trough-peak significances. Even though all significance levels were included in the cluster, the $\alpha = 0.20$ level for method 7 formed a subcluster along with the methods with no significance criteria on trough-peaks. The remaining ANP estimates by these methods formed subclusters by method. Additional evidence for the dominating influence of litter on the results from method 5 are provided by the fact that method 9 was also not included in cluster D. The results of method 9 comprised cluster B. The disparity between the trough-peak analysis without significance level and with $\alpha = 0.20, 0.10$, and 0.05 levels within this cluster also reflects the influence of litter. Any significance level criterion excludes a large number of the positive increments from the calculations.

Methods

```
        5 9 9 9 9  1 2 3 4 10 11 6 7 7 8 6 6 6 7 7 8 8 8 12 12 12 13 13 13 12 13
        a b c d                a a b a b c d c d b c d a b c a b c d d
0.994 · · xxx ·
0.991 · · xxx ·                                        xxx
0.986 · · xxx ·                                        xxx          xxx
0.985 · · xxxxx·                                       xxx    xxx    xxx
0.982 · · xxxxx·                               xxx     xxx    xxx    xxx
0.979 · · xxxxx·                       xxx · xxx       xxx    xxx    xxx
0.969 · · xxxxx·      xxx · xxx · xxx                  xxx    xxx    xxx
0.968 · · xxxxx·      xxx · xxx · xxx                  xxxxx  xxx    xxx
0.962 · · xxxxx·      xxx · xxx · xxx                  xxxxx xxxxx   xxx xxx
0.956 · · xxxxx·      xxx · xxx · xxx · xxx  xxxxx xxxxx   xxx xxx
0.954 · · xxxxx·      xxx · xxx · xxx · xxx  xxxxx xxxxx  xxxxx xxx
0.945 · · xxxxx·      xxx · xxx · xxxxx xxx  xxxxx xxxxx  xxxxx xxx
0.939 · · xxxxx·      xxx · xxxxx xxxxx xxx  xxxxx xxxxx  xxxxx xxx
0.919 · · xxxxx·  xxx xxx · xxxxx xxxxx xxx  xxxxx xxxxx  xxxxx xxx
0.916 · · xxxxx·  xxx xxx · xxxxxxx xxxxx xxx xxxxx xxxxx  xxxxx xxx
0.910 · · xxxxx·  xxx xxx xxxxxxx xxxxx xxx xxxxx xxxxxxxxxx xxx
0.908 · · xxxxx·  xxx xxx xxxxxxx xxxxx xxxxxxxx xxxxxxxxxx xxx
0.881 · · xxxxx xxx xxx xxx xxxxxxx xxxxx xxxxxxxx xxxxxxxxxx xxx
0.879 · · xxxxx xxx xxx xxx xxxxxxx xxxxx xxxxxxxx xxxxxxxxxxxx
0.878 · · xxxxx xxx xxx xxx xxxxxxx xxxxxxxxxxxx xxxxxxxxxxxx
0.839 · · xxxxx xxx xxxxxxx xxxxxxx xxxxxxxxxxxx xxxxxxxxxxxx
0.806 · xxxxxxx xxx xxxxxxx xxxxxxx xxxxxxxxxxxx xxxxxxxxxxxx
0.767 · xxxxxxx xxx xxxxxxx xxxxxxxxxxxxxxxxxxx xxxxxxxxxxxx
0.688 · xxxxxxx xxxxxxxxxxx xxxxxxxxxxxxxxxxxxx xxxxxxxxxxxx
0.641 · xxxxxxx xxxxxxxxxxx xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
0.638 · xxxxxxxxxxxxxxxxxx xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
0.606 · xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
0.207 xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx
        A    B       C        I        D            I    E
```

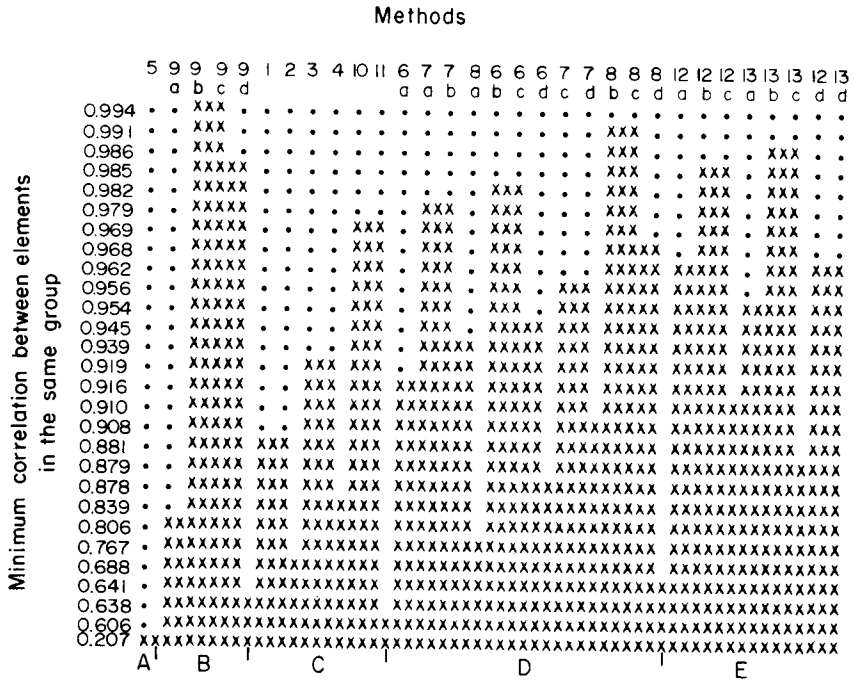Minimum correlation between elements in the same group

Fig. 11. Cluster analysis across sites, years, and treatments for 31 NPP calculations.

Cluster C includes four methods not involving trough-peak analysis and trough-peak analysis on live biomass by species (method 10) and live plus recent dead biomass by species (method 11). Within this cluster, methods 10 and 11 are most similar ($r \geq 0.97$) and under-standably more strongly correlated with methods 3 and 4 ($r \geq 0.84$) than with 1 and 2 ($r \geq 0.69$).

Although results from different methods are interrelated, the choice of method of calculation can still influence scientific conclusions as shown in the result section for a number of sites. To illustrate this in a cross-site mode, results of a three-way analysis of variance on estimates obtained by methods 1, 2, 3, 4, 5, 6a, and 8c are summarized in Table II. Note that all of the above methods, except method 8, had no statistical constraints. One would conclude that the effects of years were significant if methods 1,2,3,4,5, or 8c had been chosen as the method to calculate ANP. If method 6a had been chosen, the conclusion would be that years were not significant. Similar results were found for treatments, sites, and the two-way interactions of all three factors. Only methods 4 and 8c showed significant effects attributable to treatments. Sites were significant for methods 3, 5, 6a, and 8c.

TABLE II

ANALYSIS OF VARIANCE FOR YEAR, TREATMENTS, AND SITES
(ENTRIES ARE SIGNIFICANCE LEVEL P), FOR SEVEN METHODS OF
CALCULATING ABOVEGROUND NET PRODUCTION

| Source of Variation | Method | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6a | 8c |
| Year | 0.00 | 0.01 | 0.00 | 0.00 | 0.02 | 0.92 | 0.00 |
| Treatment (Trt) | 0.52 | 0.48 | 0.28 | 0.00 | 0.90 | 0.49 | 0.02 |
| Site | 0.80 | 0.23 | 0.00 | 0.10 | 0.00 | 0.06 | 0.03 |
| Year × Trt | 0.99 | 0.94 | 0.52 | 0.07 | 0.95 | 0.12 | 0.65 |
| Year × Site | 0.11 | 0.14 | 0.00 | 0.25 | 0.01 | 0.57 | 0.66 |
| Trt × Site | 0.20 | 0.29 | 0.00 | 0.57 | 0.04 | 0.67 | 0.06 |

The next question that we will take up is whether or not there is a rationale for calculating ANP using more complex methods over simpler ones. Part of this is answered in the cluster analysis. For example, a trough-peak analysis by species does not seem warranted over summation of species peak weights since the correlation is at least 0.84 between the two sets of estimates. Furthermore, the magnitude of the task of calculating the significances of trough-peaks by species is prohibitive, especially when the number of species is large. And if calculations are made without any statistical constraints, the estimates are questionable. Another related question is whether it is worth calculating significance levels for any of the methods involving trough-peak analyses. Results of the cluster analysis indicate that $\alpha$ = 0.20, 0.10, and 0.05 levels result in slightly different ANP estimates than the methods without any constraint on significance level of trough-peaks. An analysis of variance was performed to investigate this question further. Appropriate ANP estimates were available for the Cottonwood, Jornada, Osage, and Pantex Sites. The results are summarized in Table III. Earlier analysis of variance (Table II) of seven methods indicated differences attributable to treatments for only two of those methods, 4 and 8c. If we assume that the remaining trough-peak results will fall within the majority and show no treatment effects, then treatment results can be considered as two replicates of site-year combinations. This assumption was used in the analysis presented in Table III. The influence on the results, if the above assumption is incorrect, will be to increase the error terms and decrease the number of significances detected.

TABLE ,III

ANALYSIS OF VARIANCE FOR EFFECT OF LEVEL OF SIGNIFICANCE
IN TROUGH-PEAK ANALYSES (ENTRIES ARE SIGNIFICANCE LEVEL P)
FOR FIVE METHODS OF CALCUALTING ABOVEGROUND NET PRODUCTION

| Source of Variation | df | Method | | | | |
|---|---|---|---|---|---|---|
| | | 6 | 7 | 9 | 12 | 13 |
| Site | 3 | 0.01 | 0.04 | 0.13 | 0.17 | 0.19 |
| Year | 2 | 0.26 | 0.20 | 0.67 | 0.47 | 0.53 |
| Site × Year | 6 | 0.37 | 0.44 | 0.47 | 0.34 | 0.44 |
| Error 1 | 12 | | | | | |
| Level | 3 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Level × Site | 9 | 0.01 | 0.07 | 0.31 | 0.25 | 0.44 |
| Level × Year | 6 | 0.28 | 0.07 | 0.65 | 0.05 | 0.13 |
| Level × Site × Year | 18 | 0.00 | 0.09 | 0.28 | 0.32 | 0.45 |
| Error 2 | 36 | | | | | |

The level of significance imposed on trough-peaks was highly significant for all methods. This indicates that different results are found when different significance level criteria are used. These results agree with the cluster analysis.

From the above we conclude that: (a) all of our methods with the exception of 5 are closely related; (b) litter is the component of aerial biomass most difficult to utilize in calculations because of its variability; (c) despite the correlation among the methods differences exist among methods, such as among the estimates from methods 6, 7, and 8; (d) complex calculations do not appear to be justified considering the high cc.relation between methods such as 3 and 10 (r $\geqslant 0.84$) even though more elaborate calculations may be intuitively satisfying; (e) in trough-peak analysis, statistical constraints are warranted. The decision as to the level of significance required in trough-peaks will depend on the precision with which the biomass has been sampled. Recall from the results section that in some sites/treatments, imposing significance levels of $\alpha = 0.1$ or $\alpha = 0.05$ reduced the estimate to zero or near zero.

This brings us to the central question of which of the methods presented in the earlier section seem to be best for estimating ANP. Unfortunately there is nothing like a "true" ANP measurement available against which estimates from various methods can be com-

pared. Consequently, any discussion of the appropriateness of a method will involve weighing relative merits and demerits of various methods. Some of this has already been discussed in the review section of the paper. The answer to the question involves a value judgment, since we have shown that while all methods except 5 are significantly correlated, significant differences still exist among estimates from different methods. From a purely utilitarian point of view the simplest method (1 or 2) may be the best choice. These methods are correlated with each other ($r \geqslant 0.88$) and significantly correlated ($\alpha \leqslant 0.01$) with all other methods. Viewing the question from a more theoretical perspective, we require an answer that combines utility with intuitive satisfaction.

There is ample logical evidence that the peak standing crop of live biomass (method 1) and the peak of live plus recent dead biomass (method 2) are underestimates of ANP. Methods 5 and 9 which included litter biomass in the calculations have been shown to be unreliable. Methods 10 and 11 may be rejected because of problems presented by applying statistical constraints on the trough-peaks. Methods 12 and 13, while satisfying several theoretical criteria, yielded estimates of ANP often lower than methods 1 and 2 and required considerably more time to calculate significance levels than did the total categories (methods 6, 7, and 8) to which they were significantly correlated ($r \geqslant 0.64$). This leaves us with five methods, two utilizing species peaks (methods 3 and 4) and three trough-peak analyses (methods 6, 7, and 8). The inclusion of the recent dead component in method 4 increased the estimate as compared to method 3 although both methods were highly correlated ($r \geqslant 0.92$).

The remaining methods, 6, 7, and 8, are all very highly correlated, especially when statistical constraints are used in the calculations ($r \geqslant 0.88$). The advantages of methods 6, 7, and 8 over methods 3 and 4 are several: (a) they do not require biomass measurements for individual species; (b) it is possible to statistically constrain the results, depending upon the precision of biomass measurements, without significantly increasing the calculation time; (c) they consider more than one growth peak per season; (d) they do not assume a zero starting point for live biomass so they can be used for estimating ANP in any time-interval. The major disadvantage is that they do not explicitly consider phenological differences among species.

Considering methods 6, 7, and 8, the latter yields the highest estimates because it takes into account the amount of material produced and transferred to the two dead compartments within a sampling interval. This method can also be applied to sites where recent dead and old dead categories have not been separated; instead significant concurrent positive increments in total live and total standing dead compartments can be summed.

TABLE IV

CONVERSION FACTORS FOR ESTIMATES OF ANP BY ONE
METHOD TO ANOTHER BY LINEAR REGRESSION THROUGH
THE ORIGIN (ALL $\alpha \leq 0.001$)

| Equation | | | Standard Error | n |
|---|---|---|---|---|
| Estimates predicted for following methods $=$ | Conversion factor $\times$ | Estimates calculated from following methods | | |
| $2^{a/}$ | $=$ 1.17 $\times$ | $1^{a/}$ | 0.05 | 30 |
| 3 | $=$ 1.26 $\times$ | 1 | 0.06 | 33 |
| 4 | $=$ 1.45 $\times$ | 1 | 0.10 | 27 |
| 6c | $=$ 0.94 $\times$ | 1 | 0.04 | 33 |
| 8c | $=$ 1.41 $\times$ | 1 | 0.08 | 33 |
| 3 | $=$ 1.03 $\times$ | 2 | 0.06 | 30 |
| 4 | $=$ 1.22 $\times$ | 2 | 0.08 | 27 |
| 6c | $=$ 0.78 $\times$ | 2 | 0.05 | 30 |
| 8c | $=$ 1.20 $\times$ | 2 | 0.07 | 30 |
| 4 | $=$ 1.16 $\times$ | 3 | 0.04 | 27 |
| 6c | $=$ 0.72 $\times$ | 3 | 0.03 | 33 |
| 8c | $=$ 1.09 $\times$ | 3 | 0.06 | 33 |
| 6c | $=$ 0.62 $\times$ | 4 | 0.04 | 27 |
| 8c | $=$ 0.94 $\times$ | 4 | 0.05 | 27 |
| 8c | $=$ 1.49 $\times$ | 6c | 0.05 | 33 |

[a/] See text for explanation of numbered methods.

One of the objectives of this study was to investigate whether simple conversion factors exist which could be applied to the estimate obtained from one technique to make it comparable to the estimate(s) from other method(s), especially for a cross-site analysis and synthesis. The cluster analysis indicated that it is possible to do so. Table IV includes factors for interconversion of estimates from methods 1, 2, 3, 4, 6c, and 8c. These factors were arrived at by simple linear regression through the origin.

It is evident from Table IV that methods 4 and 8c always yield the greater estimates of ANP. The nature of the relationship between the estimate of methods 4 and 8c will vary depending upon the assumed starting point. If both methods assume zero live biomass at the beginning of the season, 8c will always be equal to or greater than 4.

## VI. CONCLUSIONS

We have shown that although most of the methods used in computing net aerial primary production are correlated with each other, they may yield significantly different estimates when applied to the same set of data. Methods that yield highest or lowest estimates differ from site to site and the choice of the methods is likely to influence scientific conclusions and interpretations. Some methods appear to be better discriminators of treatments whereas others may prove more useful for distinguishing sites or years.

Justification for going from simple technique to a more elaborate one depends upon the kind of data available and the purpose to which the results will be applied. For example, conducting trough-peak analysis on individual species biomass as compared to a straight-forward summation of peak weights results in higher estimates of ANP although confidence in the latter estimates is low because of the high degree of variability associated with individual species biomass. Placing statistical constraints on the trough-peaks for each species in a multispecies community is likely to prove to be logistically prohibitive.

Of all the methods tested, the trough-peak analysis on total biomass categories with some statistical constraint as to the level of significance in trough-peak differences seems to be a logical choice from both a theoretical and utilitarian point of view. Estimates from principal methods, however, are interconvertible using conversion factors given in the paper.

## VII. ACKNOWLEDGMENTS

## SUMMARY

Methodology for calculating aboveground net production (ANP) has progressed from a single estimate of total standing crop at the end to an evaluation of multiple categories of biomass (viz. live, recent dead, old dead) by species and considering, with statistical constraints, each peak during the growing season.

We have reviewed the published methods for calculating ANP with the purpose of critically comparing them with each other and with current understanding of primary productivity.

As a further comparison of methods we have calculated net aboveground production by 13 methods on sets of harvest data collected by the US/IBP Grassland Biome. The data represent a grazed and ungrazed treatment on 10 sites of six grassland types. One to three years of data were available for each site.

A hierarchical cluster analysis showed that all methods except one were significantly correlated ($r \leqslant 0.61$). Analysis of variance indicated that although all methods were significantly correlated, there were significant differences among the methods in terms of usefulness as discriminators of sites, years, or treatments.

For various utilitarian and theoretical reasons the numbers of methods were reduced to two groups of "best estimators." One group consisted of two methods involving summation of species peaks, the first utilizing live biomass, the second live + recent dead biomass. The second group comprised three methods using trough-peak analysis on live, live + recent dead, and live + recent dead + old dead biomass. Analysis for linear relations between the "best estimator" methods and 15 abiotic variables showed many significant relationships.

## RÉSUMÉ

La méthologie pour calculer la production nette au-dessus du sol (ANP) a évolué depuis un seul calcul de la récolte totale fixe à la fin de la saison jusqu' à l'évolution de multiples catègories de poids des plantes (c'est-à-dire des plantes vivantes, mortes récemment, mortes depuis longtemps) pour chaque espèce et en tenant compte de chaque maximum pendant la saison de croissance dans les limites statistiques.

Nous avons analysé les méthodes de calcul ANP qui ont été publiées avec l'intention de les comparer les unes avec les autres avec soin et avec une connaissance actuelle de la production primaire.

Afin de faire une comparaison de méthodes plus poussée, nous avons calculé la production nette au-dessus du sol à l'aide de treize méthodes à partir de données de séries de récolte rassemblées par la US/IBP Grassland Biome. Les données représentent un traitement de broutage et de non-broutage sur dix emplacements de six types de prairies. Des données datant de un à trois ans étaient disponibles pour chaque emplacement.

Une analyse hiérarchique de groupe a montré que toutes les méthodes, à l'exception d'une seule, correspondaient de manière significative ($r \leqslant 0.61$). L'analyse de variance a indiqué que, bien que toutes les méthodes aient correspondu de manière significative, il y avait des différences d'importance parmi les méthodes quant à leur utilité en tant qu'éléments discriminatoires des emplacements, des années ou des traitements.

Pour des raisons diverses, utilitaires et théoriques, les nombres des méthodes ont été réduits à deux groupes de "meilleurs estimateurs." Un groupe consistait en deux méthodes entraînant l'addition des maximums des espèces, la première utilisant un poids de plantes vivantes, l'autre un poids de plantes vivantes et de plantes mortes récemment. Le deuxième groupe comportait trois méthodes utilisant l'analyse du point le plus bas de la courbe sur un poids de plantes vivantes, vivantes + mortes récemment et vivantes + mortes récemment + mortes depuis longtemps.

L'analyse pour les relations linéaires entre les méthodes de "meilleur estimateur" et quinze variables abiotiques ont montré beaucoup de rapports d'importance.

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