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3

Estimating Aboveground Net Primary Production in Grassland- and Herbaceous-Dominated Ecosystems

Alan K. Knapp
John M. Briggs
Daniel L. Childers
Osvaldo E. Sala

Estimating aboveground net primary production (NPP) in grasslands, particularly those in which woody plants are rare, can be accomplished with relatively straightforward procedures compared with those required in other biome types (for shrublands, see chapter 4; for forests, see chapter 5; for aquatic systems, see chapters 9–10). However, the apparent structural simplicity of grasslands, and other systems dominated by herbaceous plants, belies a host of unique and complicating factors that can introduce significant errors into aboveground NPP estimates (figure 3.1). For example, most grasslands were historically home to large migratory ungulates (Stebbins 1981; Axelrod 1985) that today have been replaced by domesticated large grazers. Accounting for the intermittent and cumulative amounts of foliage consumed by herbivores (both large and small) and potential compensatory regrowth responses by plants (McNaughton 1983; Coughenour 1985) represents a significant challenge to accurate aboveground NPP estimates in these systems.

Grasslands also have been, and still are, subject to fire at a much greater frequency than most other biomes (Whelan 1995). Fire can occur in the dormant or the growing season and, unlike grazing, rapidly and completely removes biomass. Fire can either simplify or complicate estimates of aboveground NPP, and is recognized as an important determinant of aboveground NPP in many grasslands (Knapp and Seastedt 1986). Complex interactions between the behaviors of grazers and fire (Coppedge and Shaw 1998; Knapp et al. 1999) further complicate estimates.

Typically, grasslands occupy the interior of large landmasses, and the continental climates associated with these locations accentuate extremes in temperature and water availability. Droughts in particular can alter the expected phenology of plants

Figure 3.1. Structurally, grasslands are relatively simple compared to many other biomes (top left), but inherent features of grasslands such as fire (top right) and grazing (bottom left) can influence the methods chosen for quantifying aboveground net primary production. Furthermore, many grasslands have a significant woody plant component (bottom right), which is rapidly increasing around the world (Briggs et al. 2005). Thus, methods may need to be selected to accommodate this structural component. Photo credits: (top left and right): A. K. Knapp; (bottom left): M. D. Smith (Yale University); (bottom right): J. M. Briggs.

and lead to premature tissue senescence and decomposition, thus affecting aboveground NPP sampling strategies. Fire and grazing also strongly interact with drought in ways that must be recognized in order to estimate aboveground NPP accurately.

Many herbaceous wetlands are essentially grasslands, and many of the aboveground NPP issues listed above are also challenges in these systems (chapter 7, this volume). Herbivory can be an important process in herbaceous wetlands (Kreeland and Young 1997; Evers et al. 1998; Gough and Grace 1998), particularly those of high nutrient status. Fire is also a controlling factor in many large grassland wetlands (Schmalzer and Hinkle 1992; Ford and Grace 1998; Rheinhardt and Faser 2001). Interannual variation in hydrologic drivers, including hydroperiod, salinity, and depth of inundation, may directly affect aboveground NPP rates. These controls may also be manifest indirectly, such as through changes in plant phenology (Hooper and Vitousek 1998; Din et al. 2002; Brewer 2003). In oligotrophic herbaceous wetlands, such as the Florida Everglades, dramatic and rapid shifts in plant community composition in response to subtle changes in nutrient status (Childers et al. 2003) also can complicate aboveground NPP measurements in both space and time.

Despite these challenges, consistent and accurate estimates of aboveground NPP in these different systems can be made if a few key principles and guidelines are incorporated into sampling procedures. Because grasslands are among the ecosystems most responsive to climate variability (Knapp and Smith 2001; Knapp et al. 2002), accurate estimates of aboveground NPP can be key for detecting global changes in energy flow through ecosystems.

The purpose of this chapter is to briefly review past and currently accepted methods of estimating aboveground NPP in grass and herb-dominated ecosystems, provide some guiding principles and recommendations to facilitate accurate determinations of aboveground NPP, and discuss biases and errors and sampling adequacy. For these types of ecosystems, aboveground NPP is operationally defined as all aboveground plant biomass produced during a specified interval (typically the growing season, but usually expressed on an annual basis), accounting for losses due to herbivory and decomposition when appropriate. We will focus on annual and perennial grasslands, but these principles should apply to most herbaceous-dominated systems such as old fields, tundra, and many agroecosystems. In savanna, woodland, or wetland communities with significant woody plant cover (fig. 3.1), combining methods for the herbaceous strata with those recommended for shrubs or trees (chapters 4 and 5, this volume) should permit aboveground NPP to be estimated in proportion to the growth forms present.

Key Determinants and Representative Values of Grassland Aboveground NPP

Grassland climates vary widely, and, depending on the fire and grazing regime, any of several resources (water, temperature, nutrients, light) may limit aboveground NPP (Borchert 1950; Collins and Wallace 1990; Knapp et al. 1998; Ni 2004). In most arid and semi-arid grasslands, soil moisture is primarily limiting to aboveground NPP, but even in more mesic grasslands, water can limit production in most years (Lauenroth and Sala 1992; Knapp et al. 2001). At a continental scale, annual precipitation is strongly correlated with aboveground NPP (Sala et al. 1988), whereas in many temperate and tropical grasslands, nutrients or light also can be limiting (Knapp and Medina 1999). Hydrologic conditions often exert strong control on aboveground NPP in both freshwater and estuarine herbaceous wetlands. In some cases, all of these factors can co-limit aboveground NPP simultaneously or in sequence throughout the growing season (Knapp et al. 1998). Because of the high interannual variability in climate inherent to grasslands (Borchert 1950), different controls can be the primary limiting factors in different years. As a result of variability in climate, fire frequency, and grazing pressures, estimates of aboveground NPP for grassland ecosystems can vary over an order of magnitude, ranging from <100 g m^{-2} yr^{-1} in desert grasslands and <200 g m^{-2} yr^{-1} in oligotrophic freshwater wetlands to >1500 g m^{-2} yr^{-1} in tropical grasslands, with an incredible estimate of >9000 g m^{-2} yr^{-1} in a perennially wet tropical grassland (Long et al. 1989, table 3.1). Moreover, grasslands exhibit more extreme temporal variability in aboveground NPP than other biomes (Knapp and Smith 2001), and spatial variability can also be substantial (Briggs and Knapp 1995; Lauenroth et al. 1999), despite topographic gradients that are often more subtle than in other ecosystems. Because of this wide range in aboveground NPP across grasslands and the fundamental differences among determinants of this variation, sampling strategies and methods must be customized for each type of grassland.

As in most ecosystems, there are far fewer reliable estimates of belowground NPP (BNPP) in grasslands (Milchunas and Lauenroth 2001). Although there are exceptional grasslands where aboveground biomass and productivity account for 95% of the total (Long et al. 1989), it is generally accepted that a significant fraction of productivity in most grasslands occurs belowground (Sims and Singh 1978; Rice et al. 1998). Indeed, the high organic matter content of most grassland soils reflects this allocation pattern. Scurlock et al. (2002) estimated that BNPP accounted for between 40% and 90% of total NPP in grasslands globally, with BNPP greater than aboveground NPP in most grassland types. Moreover, responses and dynamics in BNPP do not necessarily mirror those of aboveground NPP; thus, aboveground NPP:BNPP ratios may not be constant (Milchunas and Lauenroth 2001; Ni 2004). Given the magnitude of BNPP in grasslands, and the direct (allocation strategies, resource uptake, etc.) and indirect (soil properties, microbial processes, etc.) effects

Table 3.1. Estimates of aboveground net primary production (NPP) for grassland sites globally

Grassland Type	Mean ($g\ m^{-2}\ yr^{-1}$)	Range	References
Hot desert	94, 148, 184, 229	16–292	Webb et al. 1983 Knapp and Smith 2001
Cold desert steppe	109, 188	69–330	Scurlock et al. 2002 Webb et al. 1983
Temperate steppe	94, 116, 189, 388	18–986	Scurlock et al. 2002 Webb et al. 1983 Knapp and Smith 2001 Lauenroth and Sala 1992
Temperate mesic	277, 354, 443, 508	197–1072	Scurlock et al. 2002 Webb et al. 1983 Knapp and Smith 2001
Subtropical savanna	316, 518, 553	80–1121	Scurlock et al. 2002 Knapp and Medina 1999
Tropical wet	732, 3223	331–9425	Scurlock et al. 2002 Long et al. 1989
Herbaceous wetlands		900–5500	Mitsch and Gosselink 2000
Herbaceous oligotrophic wetlands	900, 2900, 300	150–2900	Davis 1989 Daoust and Childers 1998 Childers et al. 2003

Notes: These values were derived from a wide variety of studies employing different methods, some of which likely underestimate and others of which overestimate aboveground NPP. Data for means and ranges are based on both temporal (long-term data from one or a few sites) and spatial sampling (combining sites on different continents), and should be used only as guides for the expected magnitude of aboveground NPP encountered in different grassland types.

of BNPP on aboveground NPP, measuring BNPP is critically important for understanding ecological interactions in these ecosystems. A review of techniques and recommendations for estimating BNPP in grasslands can be found in chapter 8 of this volume.

Guiding Principles and Recommendations for Grasslands

Review of Methods

Despite the relative ease with which most grasslands can be sampled for aboveground production, temporal and spatial variability in aboveground NPP is significant, and field sampling and lab processing time can be substantial. As a result, numerous methods have been proposed, many having the goal of reducing sampling effort while optimizing the information gained from the time and resources expended to estimate aboveground NPP (Wiegert 1962; Briggs and Knapp 1991; Brummer et al. 1994). These can be divided into two general approaches to estimating aboveground NPP in grasslands: direct harvest methods and indirect or "nondestructive" techniques. Although numerous variations have been proposed for each of these approaches, we will review only a few here.

Harvest methods require the direct removal of aboveground plant biomass from plots of a specified size (usually <1 m^2), separation of this biomass into components (live vs. dead, by growth form, by species), drying to a constant mass, and weighing. Variations in this method involve plot size, shape, and number; sampling frequency; pairing plots in grazed systems; and the mode of biomass harvest (Wiegert 1962; Van Dyne et al. 1963; Kelly et al. 1974; Singh et al. 1975; Dickerman et al. 1986; Brummer et al. 1994). Harvests are typically accomplished with handheld scissors, but because harvesting of biomass in this way can be quite time-consuming, alternative means ranging from the use of handheld electric clippers to large mowers to vacuum devices have been proposed to speed the process (Van Dyne et al. 1963; Milner and Hughes 1968). Error due to spatial variability is inherent in harvest methods, and this problem is typically addressed by harvesting many plots at a time. The major labor cost is thus in the lab—in sorting and drying many samples. There are few alternatives that can substantially reduce this labor cost. A number of double sampling protocols and indirect techniques (see below) have been developed in which easily measured or estimated parameters (plant height, cover, etc.) are correlated with harvest data (Catchpole and Wheeler 1992; Daoust and Childers 1998; Vermeire and Gillen 2001). We provide more details on the harvest method below as the recommended technique for estimating aboveground NPP in most grasslands.

A second general approach, using indirect or nondestructive techniques, includes numerous variations for estimating aboveground NPP in grasslands. Among them are the use of electrical capacitance and beta attenuation devices for estimating leaf area and canopy volume as correlates of aboveground NPP (Mitchell 1972; Knapp et al. 1985; Sala and Austin 2000), point intercept methods (Catchpole and Wheeler 1992), disk pasture meters (Trollope and Potgieter 1986; Dorgeloh 2002), visual obstruction methods (Vermeire and Gillen 2001), the measurement of canopy optical properties with handheld devices or via remote sensing (Tucker 1980; Turner et al. 1992, 2005), and simulation modeling (Roxburgh et al. 2004). Indirect techniques, in which easily measured attributes are correlated with biomass, can be a preferred alternative to harvest methods in grasslands where the number of plots that must be harvested is prohibitively large due to continuous growth of the vegetation (e.g., tropical systems), where a high sampling frequency is required to account for rapid turnover of biomass, or where large harvests are difficult (e.g., in national parks). In addition, many of these indirect methods can be useful for coarse estimates of standing crop biomass and fuel loads, and it is important to emphasize that some indirect methods, such as remotely sensed "greenness indices" or NDVI, can be quite valuable for estimates across large spatial scales. This is particularly true at the regional and global scales, where standing crop is often coarsely correlated with aboveground NPP (Prince and Goward 1995). However, the uncertainty and error inherent in predicting the rate of a process such as aboveground NPP from a pool size (standing crop) are often too high for site-based ecological studies in grasslands (Turner et al. 1992, 2005). Recent advances in combining remote sensing output with process-based models may improve predictions of aboveground NPP with satellite/airborne sensors (chapter 11, this volume).

Recommended Methods

General

Approaches based on the harvest method are recommended for estimating aboveground NPP in most grasslands, with a series of modifications depending on the accuracy required, the important drivers of aboveground NPP, and the inherent attributes of a given grassland type. However, the harvest method may not be best for tropical grassland systems or any herbaceous system in which destructive harvesting is a problem. For these situations, allometric techniques that are regularly validated with harvests (e.g., Daoust and Childers 1998; chapter 7, this volume) are recommended. General principles of these methods are outlined below for different types of grasslands. These are presented from the simplest to the most complex situations.

Key to the success of most harvest methods is the ability to accurately recognize and partition aboveground biomass into three pools: green (living) biomass (b_g); senesced material produced during the current year, often referred to as current year's dead (b_{sc}) or standing dead because it usually, though not always, is elevated above the surface litter and is typically not in contact with the soil surface (however, this material need not be attached to the living plant); and dead biomass from previous years (b_l) in the form of litter on the soil surface or as standing dead material. The latter two pools may be readily distinguished on the basis of their color/appearance in many ecosystems, but may be more difficult to separate in others (Singh et al. 1975). In tropical grasslands or herbaceous wetlands, for instance, there is often little remaining of the previous year's dead material. Despite this difficulty, it is critical for investigators to be able to distinguish b_{sc} from b_l because accurate aboveground NPP estimates depend on quantifying these pools. In contrast, the simplest harvest methods are those that require measuring just green or living biomass, which is the most easily distinguished aboveground component (Singh et al. 1975; Ni 2004). Those methods that require measuring only living biomass are not appropriate for most grasslands, however. This is because there are virtually no natural grasslands where plant growth phenologies and patterns of senescence are so uniform and temporally distinct that senescent biomass can be ignored without introducing significant errors (Singh et al. 1975; Sala and Austin 2000). Intensively managed artificial grasslands, such as wheat fields and other agroecosystems, would be the exception to this rule. Thus, the harvest methods recommended all include some level of accounting for plant senescence (i.e., mortality, as per Wiegert and Evans [1964], or turnover).

Peak Standing Biomass Harvest

As the name implies, this method bases estimates of aboveground NPP on aboveground biomass harvested once, usually near the end of the growing season, at or just after the time of peak biomass. This method is recommended for grasslands that meet the following criteria: (1) there is little carryover of living biomass from previous years due to a distinct dormant season or fire during the dormant season, or the previous year's biomass can be easily recognized and separated from the current year's biomass (living and dead); (2) the growing season is sufficiently short or plant material is of such low quality that decomposition of biomass produced during the growing season can be ignored; (3) consumption of plants by herbivores is minimal (i.e., large grazers are absent and small vertebrates and invertebrates can be ignored). If these criteria are met, or if the errors associated with relaxing them are acceptable, then green and current year's standing dead biomass at the time of harvest can be summed to estimate aboveground NPP. Hence,

$$\text{Aboveground NPP} = b_g + b_{sc}$$

This method has been used extensively at the Konza Prairie long-term ecological research site in the central United States, where C_4 grasses dominate productivity, and fire in the dormant season is frequent (Briggs and Knapp 1995). In this grassland, there are early-season C_3 forb species that are not entirely accounted for during a single end-of-season biomass harvest, but early-season sampling of their productivity indicate that they comprise <5% of total aboveground NPP (Briggs and Knapp, unpubl. data). Thus, the effort required to include this component was deemed excessive relative to the increase in accuracy gained.

Sequential Biomass Harvests

This more labor-intensive method requires that aboveground biomass be harvested at two or more times during the growing season, typically coinciding with peaks in productivity of species with distinct phenologies. For example, if a distinct C_3 cool-season flora dominates aboveground NPP in the spring and a C_4 warm-season flora dominates in the summer, then the positive differences in green biomass are summed.

An initial harvest may also be made at the beginning of the growing season to estimate beginning biomass if some carryover of living biomass occurs. This method is recommended for grasslands that meet the following criteria: (1) biomass produced in previous years is present but cannot be distinguished from current-year production later in the season, and thus an initial standing biomass value may be needed to correct for this carryover biomass; (2) the grassland is composed of species with substantially different seasonal patterns of growth (cool- and warm-season species, C_3 vs. C_4 plants, etc.), and each contributes significantly to aboveground NPP; (3) consumption of plants by herbivores is minimal (i.e., large grazers are absent and small vertebrates and invertebrates can be ignored). In this method, green pools are measured at each sampling period, and these are summed over the season to estimate aboveground NPP. Hence,

$$\text{Aboveground NPP} = (b_{g2} - b_{g1}) + (b_{g3} - b_{g2}),$$

where 1, 2 . . . refer to sampling periods. ANPP is the sum of the positive values of these differences when $b_{gn} - b_{gn-1} > 0$.

In some cases, investigators may want to sample numerous times during the growing season (Singh et al. 1975), but care must be taken with such frequent sampling because both under- and overestimates of aboveground NPP can result (see below and Sala and Austin 2000 for excellent analyses of these potential errors).

Aboveground Biomass Harvest(s): Accounting for Decomposition

If production and subsequent disappearance (decomposition) of plant material are likely to be substantial during the sampling interval, then an estimate of the dynamics of all three biomass pools, as well as decomposition losses, must be made and used to account for the turnover of biomass. Wiegert and Evans (1964) proposed a method to account for decomposition in old fields dominated by grasses by harvesting biomass at frequent intervals and sorting it into live (b_g) and dead (b_{sd} and b_l) components. They also measured decomposition either with litterbags or through the disappearance of dead biomass in paired plots where all living biomass had been removed (plots were paired with those in which all biomass was harvested). By accounting for changes in live biomass between intervals and the mortality of live material (defined by changes in the standing crop of dead material, adjusted for decomposition), they calculated aboveground NPP by summing positive growth increments. In practice, pairing plots with identical characteristics (required for this technique) is almost impossible, and other approaches have been favored (Singh et al. 1975). Lomnicki et al. (1968) suggested a simplifying modification to the Wiegert-Evans method. They proposed accounting for the mortality (senescence) of live plant material by removing all dead material at the beginning of the sampling interval and then, for each sampling interval, summing living and dead material (which could have been produced only during the current growing season) in harvested plots. Although they argued that for their grassland, removing the previous year's litter had no effect on the current year's production, the key role that litter (detritus) can play in affecting microclimate, nutrient cycling, water relations, and, ultimately, aboveground NPP has been well documented in other grasslands (Knapp and Seastedt 1986). Thus, this method is not recommended.

Long et al. (1989) reviewed the extensive studies of Singh et al. (1975) and many others, and concluded that in grasslands with long growing seasons (i.e., some temperate and most tropical grasslands) and where there are long time intervals between harvests, so that losses due to decomposition will occur, the best method for estimating aboveground NPP (with the fewest assumptions) involves simultaneous measurements of changes in all plant biomass components and decomposition. This approach, which includes the basic elements of the Wiegert and Evans (1964) method, has substantial merit. Changes in mass of both living and dead pools are measured at intervals appropriate for the grassland under study, and losses due to decomposition are added to the net change in biomass. Estimating and correcting for losses due to decomposition can be time-consuming and introduce additional uncertainty (see Harmon et al. 1999 for a review of methods). However, in some wet tropical grasslands, decomposition during the growing season can be so rapid and of such a large magnitude that failure to account for this process can lead to significant underestimates in aboveground NPP (Long et al. 1989). Hence,

$$ANPP = \sum_{i=1}^{n} \Delta b_t + d,$$

where d = loss due to decomposition during the sampling interval and aboveground NPP is summed over i sampling intervals. The decision of whether or not to include nonstatistically significant changes in any component between samples should be based on the length of the sampling interval (and hence the amount of change expected) and the sample size (relatively small changes require very large sample sizes if spatial heterogeneity is high [Scurlock et al. 2002]).

Aboveground Biomass Harvest(s): Accounting for Grazing

Herbivory (mostly by large mammals in terrestrial systems and mostly by small mammals or insects in wetlands) is a widespread determinant of grassland aboveground NPP. Unfortunately, this key biotic factor complicates estimates of aboveground NPP more than any other factor discussed thus far. This is because the act of grazing (consumption) can be a continuous or intermittent process, and is almost always spatially heterogeneous. Of course, regrowth responses of the plants mirror the activities of the grazers, and both consumption and regrowth must be accounted for in aboveground NPP estimates (McNaughton et al. 1996). It is well established that plants have numerous compensatory responses to herbivory (McNaughton 1983), and simply measuring aboveground NPP in permanent or season-long grazing exclosures will not capture alterations in productivity manifest under grazed conditions. Thus, estimating aboveground NPP in grazed grasslands requires a substantial number of temporary, movable exclosures that allow for estimates of consumption by herbivores and regrowth responses of grazed plants.

This method is recommended with either of two variations. In grasslands actively grazed by large herbivores, a large number of temporary exclosures are randomly placed for a relatively short period of time (1–2 weeks). At the end of this period, all living and current year's senesced biomass within the exclosures is harvested. If a similar harvest is made at the same time outside the exclosures, an estimate of consumption can be made; these estimates can be summed for all intervals and added to residual biomass at the end of the season to estimate aboveground NPP. Hence,

$$\text{Aboveground NPP} = \Sigma C + (b_g + b_{sc})_{final},$$

where C = consumption and "final" refers to standing crop biomass at the end of the year (or growth season). Decomposition of current-year growth is assumed to be unimportant if grazing intensity is high or the growth season is relatively short (Frank and McNaughton 1993).

A variation of this method involves harvesting plots outside the exclosures at the beginning of the interval rather than at the end, when exclosed biomass is harvested. This approach measures regrowth within the exclosures during the interval rather than consumption. The sum of these estimates comprises aboveground NPP for the season. Exclosures should be placed prior to growth at the beginning of the growing season (such that the initial measures of b_g and b_{sc} outside of exclosures is zero), and continue to be harvested and moved at regular intervals until the end of the season or year. Hence,

$$\text{Aboveground NPP} = \Sigma\,[(b_g + b_{sc})_{ex} - (b_g + b_{sc})_{outside}],$$

where exclosure (ex) biomass is harvested at the end of intervals and outside biomass is harvested at the beginning of the interval.

There are also unique situations that may require combinations of methods or additional alterations (Cox and Waithaka 1989). For example, in lightly and patchily grazed grasslands, ungrazed areas may require methods different from those used in grazed areas. Indeed, it is advisable to estimate grazing pressure prior to selecting a sampling method and estimating the number of plots needed. Heavily and uniformly grazed grasslands will require fewer exclosures and plots than patchily grazed systems (McNaughton et al. 1996) but, as noted earlier, each grassland will require a unique sampling scheme. Table 3.2 summarizes some of the characteristics of grasslands that are important to consider when choosing among the four primary methods for estimating aboveground NPP reviewed above.

Additional Methodological Issues

This chapter does not provide a detailed methodological discourse on field harvesting, processing biomass from plots, the selection of the optimal plot size and shape, or the best temporal and spatial sampling strategies for estimating aboveground NPP in grasslands. This is because there are other works that provide such detail (Van Dyne et al. 1963; Milner and Hughes 1968; Dickerman et al. 1986; Brummer et al. 1994; Wiegert 1962) and because grasslands vary in so many different ways (e.g., dominance by rhizomatous vs. caespitose grasses, annual vs. perennial, desert vs. tropical wet grasslands vs. herbaceous wetlands) that specific techniques must be customized for each grassland type. Instead, the focus is on a few methodological

Table 3.2. General guide for determining the most appropriate method of estimating aboveground NPP in grassland ecosystems based on key attributes of the site

Grassland Criteria	Peak Biomass	Sequential Harvest	Sequential Harvest + Decomposition	Temporary, Movable Exclosures	Nondestructive Phenometric
1. Relatively short, distinct growing season with no carryover of live biomass	✓				
2. Decomposition not important during sampling interval	✓	✓			
3. Grazing not important	✓	✓	✓		
4. Current year senesced biomass (b_{sc})* can be distinguished from previous year's litter (b_l)**	✓				
5. Long growing season with plants having distinct phenologies, >1 peak in biomass, or carryover of live biomass from the previous year		✓	✓		✓
6. Long growing season and b_{sc} cannot be distinguished from b_l by season's end		✓	✓		
7. Decomposition of current year's production must be accounted for during the sampling interval			✓		
8. Continuous growth, low species diversity, perennial forms					✓
9. Consumption of current year's production by grazers is substantial				✓	

Note: If grazing is not important in a given grassland site, any of three methods may be selected, depending on the other criteria listed. If decomposition must also be accounted for in this site, then only one method is appropriate.
*b_{sc} = biomass produced during the current year that has senesced
**b_l = litter or dead biomass produced in years prior to the current year

details that, if overlooked, are likely to lead to systematic errors in aboveground NPP estimates. In addition, a case study is provided as a guide for how to determine an appropriate sampling effort for ecological studies that include estimates of aboveground NPP. Although the results of this case study are specific to one grassland, it serves as a relatively detailed model for quantifying and reducing sampling error in aboveground NPP estimates.

As noted earlier, correctly partitioning harvested biomass into green (b_g), senescent (b_{sc}), and previous year's dead (b_l) components can be critical for accurate aboveground NPP estimates. Operationally, defining green biomass as any plant material (foliage or stems) that contains visible chlorophyll is recommended, even if the majority of the tissue is senesced and brown. There is no loss of accuracy with including leaves that are 95% brown and 5% green in the b_g category because b_{sc} and b_g are subsequently combined to estimate aboveground NPP. Further, the presence of green tissue usually ensures that the biomass was produced that year. An exception to this rule must be made for grasses that form aerial tillers in subtropical and tropical climates. In this case, care must be taken to separate these tillers from the senescent stalk that was produced the previous year. As noted earlier, b_{sc} and b_l can usually be distinguished by color, with b_l darker brown or gray, depending on the state of decay. Sorting biomass into these categories, at least coarsely, while harvesting in the field is also recommended. It is often much easier to distinguish b_{sc} from b_l in the field than in the lab. A secondary check of the accuracy of this rough field sorting should be performed in the lab.

Greig-Smith (1983) and others (Sala and Austin 2000) have emphasized the need for sampling plot (and hence quadrat) sizes to be larger than the average plant size, which is not difficult in grasslands. However, when harvesting biomass, strict rules must be followed in defining the edge of the sampled plot and for determining if plant material is to be included or excluded from harvest. At the edge of quadrats, it is recommended that the basal portions of plants, not canopy position, be used to determine if material is to be harvested or excluded. Thus, when locating the quadrat, care should be taken to ensure that it rests on the soil surface as much as possible, and that plants are harvested from their base. Thus, canopy foliage that occurs within the vertical projection of the quadrat, but whose basal contact with the soil is outside the quadrat, would not be included. Conversely, the foliage of plants whose bases are within the quadrat would be harvested even if this foliage extends outside the vertical projection of the plot. Quadrat edges that fall across the bases of large caespitose grasses will require that only those portions of the individual bunch within the plot be harvested. In other biomes or when sampling other growth forms, alternative rules for determining portions of plants to harvest may be employed (see chapter 4, this volume). Clearly, the use of consistent methodology by all field personnel is crucial to avoid unnecessarily high variances in aboveground NPP estimates in any biome.

Long-term studies of aboveground NPP present additional challenges due to the potential cumulative effect of sampling (biomass removal) and investigator trampling on the plant community. When a site is considered for long-term sampling, sampled plots need to be marked with flags or metal tags to ensure that no further sampling takes place in that year and for at least two additional years. Thus, the size of the overall sampling area must be sufficient to accommodate harvests more than once during the season and for several years without resampling the same plot.

Errors in Estimating Aboveground Net Primary Production

Estimates of aboveground NPP (ANPP) have several sources of error that can be classified in two types: errors leading to underestimation (ELUs) of ANPP and errors leading to overestimation (ELOs) of ANPP (Sala et al. 1988). These two types of errors are different in nature and will be discussed separately.

Errors Leading to Underestimation

Errors leading to underestimation of aboveground NPP result from two sources: missing peaks of biomass and the simultaneous nature of production, senescence, and decomposition. The first source of error can be reduced by a high frequency of sampling that reduces the possibility of missing peaks of biomass, and the consequent underestimation of annual aboveground NPP. The second source of error is associated with the simultaneous nature of production and senescence, and is also conceptually very clear. Solutions to address this issue have been to simultaneously estimate biomass of different species and different categories, such as green, current years and previous years dead biomass. The combination of high frequency and sampling several species and types of biomass should result in a reduction of ELUs.

Errors Leading to Overestimation

Errors leading to overestimation were first recognized by Singh et al. (1984) and Lauenroth et al. (1986). ELOs result from the fact that random errors in estimates of biomass inevitably accumulate but may not compensate for each other, leading to a positive bias in the estimates of ANPP. Sala et al. (1988) analytically determined that aboveground NPP, defined as the increase in positive biomass increments during periods of time, is a biased estimator of the true net primary production. When biomass at time t+1 is larger than biomass at t_0, we consider that $B_{t+1} - B_{t0}$ is the estimate of NPP. When B_{t+1} is less than B_{t0}, we consider that production and growth have been zero. Biomass estimates are random variables, but this error accumulates in the estimate of NPP. For example, assume that the true value $B_{t+1} = B_{t0}$ and consequently the true NPP = 0. However, because B is a random variable, in some instances B_{t+1} will be higher than B_{t0} and in other instances B_{t+1} will be lower than B_{t0}. The NPP bias occurs as a result of the fact that most sampling protocols require that all the negative values ($B_{t+1} < B_{t0}$) be discarded, but that all positive values ($B_{t+1} > B_{t0}$) be included.

Singh et al. (1984) and Lauenroth et al. (1986) performed modeling experiments in which they simulated a true value of production and calculated the magnitude of the ELOs by randomly sampling from a true distribution. These experiments indicated that the magnitude of the ELOs could be quite large. For belowground productivity, estimates of NPP were 5 times higher than true NPP, and for aboveground NPP the estimated value was 33% higher than the true value.

Sala et al. (1988) analytically derived the distribution function of the estimator of NPP, which is nonnormal, and concluded that the estimator is a biased estimate of productivity. From the distribution function of NPP, it was possible to derive the equation to calculate the magnitude of the overestimation error (OE):

$$OE = (\sigma / \sqrt{2\pi})\, e^{-\frac{1}{2}(\mu/\sigma)^2} - q\mu$$

This equation yields interesting conceptual results. The magnitude of the overestimation error is a function of (1) the magnitude of the standard deviation (σ) of NPP that is directly related to the magnitude of the error in estimating biomass (B_{t+1} and B_t), and (2) the true value of NPP (μ). The magnitude of the overestimation error increases as the error increases and as the true value of NPP decreases. Consequently, methods that try to reduce ELUs by increasing the sampling frequency will necessarily increase the ELOs because as the sampling frequency increases, the true value of productivity decreases. The magnitude of the true increase in biomass decreases as the sampling dates get close to each other. Similarly, methods that choose to estimate biomass by species result in larger ELOs because the true value of $B_{t+1} - B_t$ is lower for subunits such as a species than for functional groups or total biomass. ELOs are lower when aboveground NPP is estimated from differences in total biomass than when it is estimated from differences in biomass per species that then are added.

The paradox is that those techniques devised to reduce one kind of error (ELUs) inevitably result in the increase of the other kind of error (ELOs). The same is true of efforts aimed at reducing ELOs that result in high ELUs. Biondini et al. (1991) developed an algorithm that can be used to estimate the magnitude of the ELOs based on the observed mean of aboveground NPP and the observed standard deviation. This algorithm allows for correction of the OE and for focusing on reducing the ELUs.

This analysis of ELOs and ELUs shows that methods that are more complicated and conceptually more complete may not necessarily yield results closer to the true value of aboveground NPP than simpler methods. In many cases, elaborate and expensive methods based on high frequency of sampling and estimates per species yield results farther from the true aboveground NPP than those yielded by simpler methods.

Determining Sample Adequacy: A Case Study

Below, a case study is presented that determined the appropriate level of sampling needed to reliably estimate aboveground NPP in tallgrass prairie. This analysis focused on determining the effect of varying sample sizes on aboveground NPP estimates and the impact of sample size on the statistical determination of the response of this ecosystem to fire. The case study, a summary of Briggs and Knapp (1991), used a combination of jackknifing and Monte Carlo simulations based on sampling of aboveground NPP over a 14-yr period. As mentioned earlier, Wiegert (1962) discussed the trade-off between many small and few large quadrats when calculating variance for biomass estimates. This analysis did not include variables such as plot size, shape, and area, and sampling protocol, but instead focused on a single quadrat size (0.1m^2) used extensively in estimating aboveground NPP in tallgrass prairie (Hulbert 1969; Barnes et al. 1983; Abrams et al. 1986; Steuter 1987; Briggs et al. 1989; Briggs and Knapp 1995; Briggs and Knapp 2001). This size quadrat fits the criteria of Greig-Smith (1983) regarding the relationship between quadrat dimension and average plant size. A three-sided metal frame (a rectangular quadrat with one open end) was used that allowed the frame to be easily inserted into dense vegetation.

Research was conducted at the Konza Prairie Biological Station, in a C_4-dominated grassland with a typical Midwestern continental climate characterized by warm, wet summers and dry, cold winters (Knapp et al. 1998). Fire is critical to the maintenance and functioning of tallgrass prairie (Collins and Wallace 1990), and since 1981 (and in some areas on Konza since 1971) entire watersheds have been subjected to late spring (April 10 ± 20 days) fires at intervals of 1, 2, 4, 10, and 20 yrs.

Although estimates of aboveground productivity are made in numerous watersheds on Konza Prairie, analyses for this study were limited to a unique data set from two intensively studied watersheds. One watershed (hereafter referred to as the high-fire-frequency site) had been burned annually for > 20 years, and the adjacent watershed (hereafter referred to as the low-fire-frequency site) had been burned only once in 20 years (1994). Beginning in 1984 and continuing until 1997, 20 0.1-m^2 plots were harvested at about 2-wk intervals from May to September in these two adjacent watersheds. Soil type and topographic position were similar at both sites of biomass harvest. Detailed methodology for sampling the aboveground components are given in Abrams et al. (1986), Briggs and Knapp (1995), and Knapp et al. (1998). Briefly, all harvested plant material was first separated into live (at least partially green), current-year senescent, and previous-year(s) dead biomass (on unburned sites). Live plant material was further separated into graminoids (dominated by C_4 plants) and forbs (primarily C_3 plants, including a minor woody plant component (less < 5%). All material was oven-dried at 60° C for 48 hr, and weighed to the nearest 0.1g, with values expressed as g/m^2. Although permanent sites were used in this study, the plots sampled biweekly were marked so that resampling of specific locations could be avoided for several years.

Sample adequacy was determined in two ways. First, a running mean and the standard error of the mean were plotted for sequentially sampled quadrats. When the standard error of the mean was reduced to <10% of the mean, it was concluded that the sample size was sufficient (National Academy of Sciences 1962). In addition, jackknifing techniques were used to randomly select data with samples sizes of 2 to 18, and again a standard error of <10% was used as the criterion for sample adequacy. This analysis was replicated 20 times, with a maximum and a minimum standard error (SE) for each sample size determined.

To examine the effect of sample size on the statistical detection of treatment effects (fire, in this case), data sets were used from this jackknifing analysis, and t-statistics were computed for each sample size (total of 720 t-tests). Since all variables (total aboveground, grass and forb biomass) were significantly different at a sample size of 20, the sample size was deemed adequate if all 20 randomly generated comparisons were also significantly different at $P = 0.05$. Finally, since the effect of fire on biomass in tallgrass prairie can vary by over 60% (Knapp et al. 1998), the analysis was extended using Monte Carlo simulations. Simulations were begun with mean biomass values from a long-term record for both upland and lowland soil types under high fire frequency and low fire frequency. These mean values were adjusted to obtain a 10%, 20%, 30%, and 40% increase in biomass in burned relative to unburned sites. Variances were also adjusted on the basis of long-term data sets. Similarly, when the sample size was decreased to determine its effect on statistical comparisons, the sample variance was also increased. This was accomplished with data from the jackknifing exercise. Maximum variances were used to ensure that sample adequacy estimates were as conservative as possible.

When the running mean was calculated for sequential quadrats, the standard error of the mean decreased to <10% of the mean at 10 quadrats for the high-fire- frequency site and 18 for the low-fire-frequency site. Based on the jackknifing analysis, 14 and 16 quadrats were deemed adequate (maximum SE <10% of the mean) for estimating aboveground NPP in the high- and low-fire-frequency sites, respectively. The random ordering of the plots and the large number of repetitions generated via this jackknifing procedure provided greater confidence in this recommended sample size.

Results of analyses on the effect of sample size on the statistical detection of treatment effects were specific to the particular components of aboveground NPP that were being estimated. For example, if only the grass component was of interest, a sample size of 14 was deemed adequate. But if differences in total aboveground NPP were of interest, a sample size of 18 was necessary, with 30 quadrats required for reliable statistical comparisons of the forb component. Overall, results indicated that to detect a treatment effect on aboveground NPP with a magnitude of 20%, a sample size of 20 quadrats (0.1 m^2) was required (fig. 3.2). Since a sample size of 20 is near the inflection point of the relationship in figure 3.2, it may represent the optimal sample size (for 0.1 m^2 quadrats) for assessing fire effects in this tallgrass prairie.

Based on these analyses, it is recommended that to estimate aboveground NPP with an SE of the mean of <10% of the mean, 14 and 16 quadrats should be harvested from burned and unburned sites in tallgrass prairie, respectively. If the goal of aboveground NPP estimates is to detect treatment effects due to fire, at least 20 quadrats (0.1 m^2) would have to be harvested per site. Finally, these results suggest that a treatment effect of <20% would be very difficult to detect using aboveground NPP as the response variable in this grassland. Moreover, because forbs are patchily distributed and are a relatively small component of aboveground NPP, only large changes in this growth form component could be detected with a sampling effort deemed adequate for total aboveground NPP.

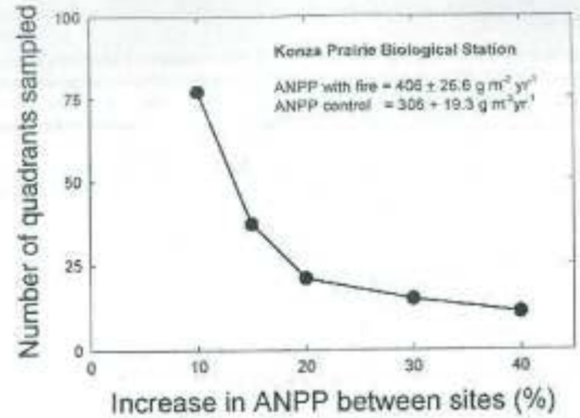

Figure 3.2. The relationship of the magnitude of change in aboveground net primary production (ANPP) between burned and unburned sites in a mesic grassland (Konza Prairie, Kansas) and the number of quadrats that would need to be sampled to statistically detect this change. This analysis was based on long-term field estimates of ANPP in response to fire and on Monte Carlo simulations in which sample size and variances were adjusted (see Briggs and Knapp 1991 for more details).

Final Comments

The goal of this chapter was to provide guiding principles for estimating aboveground NPP in grasslands, not detailed methods. Even cursory consideration of the varied attributes of grasslands and the number of potential determinants of productivity should convince the reader of the difficulty in providing detailed recommendations that would be useful for more than a few types of grasslands. Alternatively, brief coverage of those factors (herbivory, decomposition, fire, phenology, etc.) are included that, if not considered, are likely to lead to substantial errors in aboveground NPP estimates. Then, by providing guiding principles for coping with potential errors in aboveground NPP estimates, some unique to grasslands and some more general, investigators can make informed decisions when selecting the best method to adopt for their system. A summary of the primary methods recommended, and a general guide for selecting among them, are presented in table 3.2. For each of these methods, corresponding grassland attributes are indicated.

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4

Estimating Aboveground Net Primary Production in Shrub-Dominated Ecosystems

Donald R. Young

Measurement of production in shrub communities may be difficult, but it is not impossible (Whittaker 1961). Estimating aboveground net primary production (ANPP) in shrub-dominated ecosystems can be quite challenging relative to other biome types. The inherent structural complexity of shrubs, especially those with multiple stemmed bases and a high degree of vegetative propagation, frequently leads to dense communities and sampling challenges. Perhaps most reflective of these statements is the dearth of published estimates for shrub ANPP.

Shrub-dominated ecosystems span a variety of climates, including the chaparral and matorral of Mediterranean climates; the floristically diverse fynbos and Renosterveld vegetation groups; arid communities associated with deserts, steppes, and lower montane zones; maritime shrub thickets; and riparian communities including many at high elevations and high latitudes. The shrub growth form is also an important component of many biomes, such as forests and grasslands, and frequently represents a midsuccessional seral stage.

The purpose of this chapter is to review methods for estimating ANPP in shrub-dominated ecosystems and to provide guiding principles and recommendations to facilitate accurate determinations of ANPP. For these systems, ANPP is defined as all aboveground plant biomass produced per unit area during a year, accounting for losses due to herbivory and decomposition when appropriate. In most systems, production may be restricted to intervals of favorable climate during the year; nevertheless, ANPP is expressed on an annual basis. The focus of this chapter will be ecosystems in which shrubs are the dominant growth forms, but these principles should apply to the shrub component of all ecosystems. In prairie or forested communities, combining shrub methods with those for grasslands and