TOPIC 1. PRIMARY PRODUCTION AND FORAGE IN DIFFERENT PLANT COMMUNITIES

Measurements of primary production on a global scale are pertinent to the calculation of the carrying capacity of all species present of this globe. Wild ruminants are limited to certain areas of the globe and to the lower one to three meters of the biosphere. Further, wild ruminants are selective in their food habits, taking selected plant species, in different orders of preference, and then only certain parts of the plants. Therefore, measurements of primary production available to wild ruminants are limited to ruminant forage, generally considered to be just part of the available current annual growth.

Measurements of forage produced can be made directly or indirectly. Direct measurements include the cutting, drying and weighing of the plant material to determine the mass present. Indirect measurements include the measurement of certain characteristics of the plant material, such as lengths and diameters of twigs, to estimate the mass present, or the visual estimation of densities of the vegetation to come up with yield figures. Direct measurements are very time-consuming but more precise than indirect measurements. The latter can be very quick and, with the proper experience, fairly accurate.

My personal evaluation of the use of direct and indirect measurements includes the use of direct measurements to gain experience with vegetation densities and mass, followed by derivation of decision-making procedures for indirect measurements. Such procedures should include successive stages in the decision-making process that are, by themselves, relatively easy to make, and which, in the entire sequence, lead the evaluater to the right response. I compare such a procedure for estimating forage to a dichotomous key for identifying plants; each decision is made on the basis of evidence for one or the other answer, and the order of questions and answers leads to the right conclusion.

It is necessary to develop some fairly rapid means of estimating forage produced in order to get reasonable estimates distributed over space and time. Plant communities inhabited by wild ruminants are too extensive to be visited on hands and knees with clippers and collecting bag. Visual reconnaissance, photo interpretation, and satellite imagery evaluations provide potential means for estimating forage produced over large areas of space. Once such means are available over space, then estimates can be made over time, simply repeating the estimates at selected intervals to see changes due to natural succession and the effects of man's activities.

The next five UNITS contain information and references for the measurements and distributing of forage production over space and time.

Forage is generally considered to be the current years' growth of herbaceous plants and the current annual growth of woody species. That definition cannot be adhered to strictly because species which retain their leaves for more than one year and lichens which do not differentiate growth between years may be forage for some species.

UNIT 1.1: PRIMARY PRODUCTION IN DIFFERENT PLANT COMMUNITIES

Primary production varies between plant communities, with differences dependent primarily on moisture and temperature conditions during the growing season. These differences result in characteristic physical structures of the communities, with the tundra having no overhead canopy at one extreme and the coniferous forest a very dense canopy.

The discussions of each of the plant communities that follow should be accompanied by mental impressions of the life-forms of the plants and physical structures of the canopies. These characteristics affect the forage available to ruminants, and the amounts are related to the spatial distribution of forage (UNIT 1.3) and stage in succession (UNIT 1.4).

The brief discussions of different plant communities are based on Whittaker (1975) and Lieth (1975). They should be supplemented by further study in plant ecology books and references.

TUNDRA

Tundras are treeless plains in the alpine zones and in the arctic. Tundra vegetation is dominated by dwarf-shrubs, sedges, grasses, mosses, and lichens. The deep layers of the soil are permanently frozen in many areas of arctic tundra and in some alpine communities (Whittaker 1975:156). Productivity of tundra is low because only the upper layer of soil becomes biologically active each summer over permafrost. The vegetation is slow-growing and low in height.

Arctic tundra, which covers most areas of land in the northern part of the North American continent, is inhabited by caribou and muskoxen. Alpine tundra is restricted to small areas at the highest elevations in the mountains of North America. It is inhabited by sheep and goats, but these species move to lower elevations and use other habitats as well.

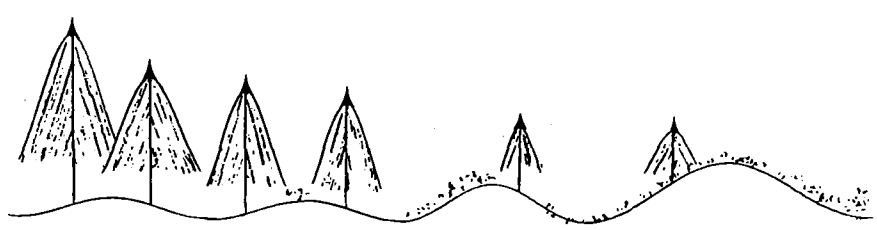
Tundra net primary productivity is very low, with less productivity observed only in desert vegetation. The approximate mean net primary productivity is 140 grams per square meter per year (Lieth 1975:205), with a range from 10 to 400 gms/square meter/year (Whittaker 1975:224). The biomass for tundra and alpine vegetation given by Whittaker (1975:224) is 0.6 kg per square meter as a mean, with a range of 0.1 to 3 kg/square meter. These values are listed in the table on the next page.

All of the tundra vegetation is within reach of foraging wild ruminants; net annual primary productivity equals forage available. Not all of the annual productivity should be consumed, of course, since the plants need reserves in order to remain productive from year to year.

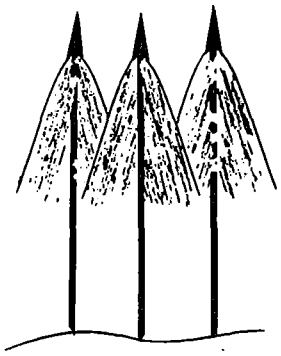
	Net primary productivity ($g/m^2/yr$)		Biomass		Reference
	mean	range	mean	range	
tundra	140				Lieth 1975:205
"		10 - 40	0.6	0.1 - 3.0	Whittaker 1975:224
boreal forest	800	400 - 2000	20	6 - 40	Whittaker 1975:224
temperate evergreen forest	1300	600 - 2500	35	6 - 200	Whittaker 1975:224
temperate deciduous forest	1200	600 - 2500	30	6 - 60	Whittaker 1975:224
woodland	600	200 - 1000	---	2 - 20	Lieth 1975
temperate grassland	600	200 - 1500	1.6	0.2 - 5.0	Whittaker 1975:224
dry	0.3	0 - 10			Lieth 1975:205
desert			0	0	Lieth 1975:207

EVERGREEN FORESTS

Evergreen forests include the taiga, subarctic-subalpine needle-leaved forests and the temperate evergreen forests. Dominant species in the taiga are spruce and fir, and in the temperate evergreen forest, pine. These forests often contain few tree species, with the understory varied depending on land soil and moisture conditions, and the density of the canopy. The taiga merges with the tundra as the trees of the taiga thin out and the tundra vegetation develops between them.

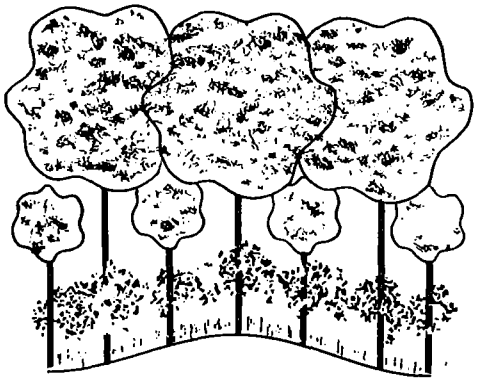


Note in the table on the previous page that both net primary productivity and biomass are larger in the temperate evergreen forest than in the boreal forest. The trees are also taller, spreading the primary productivity and the biomass over a larger vertical dimension. Some of this primary productivity is out reach of the animals (moose, for example) which inhabit these forests, and the canopy also reduces productivity in the forage production zone.



DECIDUOUS FORESTS

The temperate deciduous forest is a vegetation unit characterized by a wide variety of tree species, often organized into 4 distinct layers: a canopy with the crowns of the oldest trees, subcanopy with saplings and trees which mature in the subcanopy, shrub layer, and herb layer. The net primary productivity of such forests is high. Very little of the light that reaches the tree canopy penetrates to the herb layer, especially in the well-established stands containing the species considered characteristic of a mature or climax forest. The herb layer is most active in the spring before the canopy leafs out; an abundance of early-blooming flowers makes the temperate deciduous forest a very beautiful place in the spring.

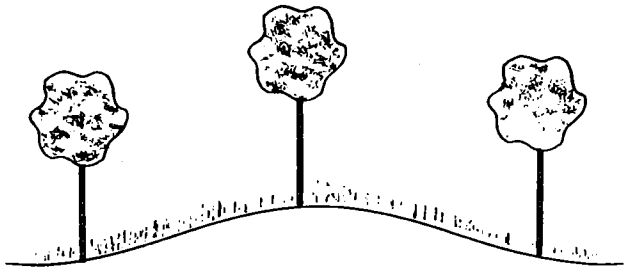


The temperate deciduous forest includes trees that produce seeds and fruits that are often readily consumed by wild ruminants. The abundance of acorns in the fall, for example, may be an important determinant of the condition of deer going into the winter. Much of the primary production in some temperate deciduous forest types is out of reach of wild ruminants, and the shrub and herb layers may be very sparse.

Deciduous forests merge into grassland on both sides of the Great Plains in the midwestern states and prairie provinces, and in other areas of North America. The transition plant community of smaller trees and variable canopy densities is called a woodland.

WOODLANDS

Woodlands are a special type of forest. The canopy may be nearly complete or quite open, with only scattered trees. Woodlands are found in climates too dry for true forests, but not dry enough to give way to grassland, shrublands, and semidesert (Whittaker 1975:139). They may have a very sparse shrub layer. The canopy may be open enough to allow grasses and shrubs to develop on the ground surface. Woodlands are sometimes park-like in their appearance. They may be pastured, and some woodlands may be maintained by prescribed burning. Woodlands mean different things to different people since they are partly a function of man's activities.



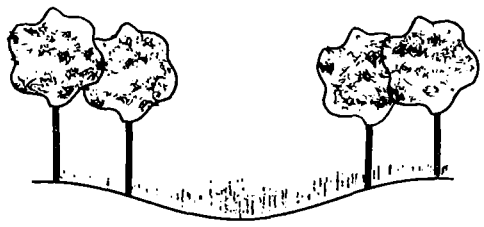
GRASSLANDS, MEADOWS, AND PASTURES

Grasslands are characteristic of dryer areas, without trees and with a sparse shrub layer. The grass and herb layers form the canopy, with a litter layer that builds up if not disturbed by grazing or fire. Overgrazing results in an increase in the shrub components, and fire is often used as a management tool to stimulate the growth of grasses and arrest invasion by shrubs.

The primary productivity of temperate grassland is very high (see the table on page 8), considering the relatively low height of the vegetation. All of the primary productivity is concentrated in a meter or two of vertical height.

Variations in net annual primary productivity of grasslands are marked along a precipitation: evaporation ratio gradient. The most favorable moisture conditions result in tall-grass prairie vegetation, and the least favorable, a short-grass prairie vegetation.

Meadows are openings in forest vegetation which may be due to natural causes, such as mountain meadows, or to clearing by man with little or no secondary successsion occurring due to revegetation by grasses and other herbaceous plants. Meadows may mean different things to different people, depending on experience and associations.



Pastures are grazed and fenced areas that are more or less intensively managed. Pastures may contain only natural vegetation, or they may be planted to selected species. Pastures in some areas include trees, with reduced primary prductivity of the pasture vegetation when it is shaded by an overhead canopy.

DESERTS

Deserts have net annual primary productivity that is very low, limited by a definite lack of moisture. They are productive only after periods of rainfall, with the native desert plants well-adapted to survival during long periods of drought. The morphology of much of the desert vegetation reflects this; plants such as cacti have very low surface areas and thick cuticles, minimizing water loss. These characteristics make the plants rather unattractive to wild ruminants.

Primary production is discussed here in UNIT 1.1 as a prelude to discussions of forage production in UNITS 1.2, 1.3, and 1.4. The next three UNITS call attention to forage production measurements, forage distributions, and forage production at different stages of succession.

LITERATURE CITED

Lieth, H. 1975. Primary production of the major vegetation units of the world. Pages 203-215 In: H. Lieth and R. H. Whittaker, Ed., Primary productivity of the biosphere. Springer-Verlag, NY. 339 pp.

Whittaker, R. H. 1975. Communities and ecosystems. Macmillan Publishing Co., N.Y. 387 pp.

REFERENCES, UNIT 1.1

PRIMARY PRODUCTION IN DIFFERENT PLANT COMMUNITIES

SERIALS

CODEN	VO-NU	BEPA	ENPA	PLCO*KEY WORDS----------	AUTHORS----------	YEAR
ABSZA	30--4	1	44	tund lichen stands, newfo, rata	ahti,t	1959
ATLPA	4---4	291	305	tund veget types & plnt biomass	wielgolaski,fe	1972
ATLPA	4---1	307	324	tund seas cours of abvgrnd prod	tieszen,ll	1972
BPURD	1----	90	94	tund effect air pollut on liche	schofield,e	1975
BOREA	10---	1	65	tund conif, lich-biol, econ sig	perez-llano,ga	1944
CAFNA	80--3	119	143	tund botan inves, subarct, sask	argus,cw	1966
CAFNA	85--1	39	52	tund lich, forage abund, newfou	bergerud,at	1971
CJBOA	41--8	1199	1202	tund growth rate, cladonia spec	scotter,gw	1963
ECBOA	10--4	367	392	tund util lichn, arct, sub-arct	llano,ga	1956
ECMOA	34--3	243	270	tund env, stand crp, prod, alpn	scott,d; billings	1964
ECOLA	52--6	1058	1064	tund eff alp plnt communs, wash	douglas,gw; balla	1971
JRMGA	23--1	8	14	tund ranges nrth of boreal fore	klein,dr	1970
JSABA	42--2	231	263	tund stan crp, nutr stat, s afr	smith,vr	1976
JSABA	43--2	105	114	tund veg stand crop, lava flows	smith,vr	1977
NOSCA	48--1	38	51	tund alpn soil, plnt comm, ovda	lord,tm; luckhurs	1974
PABCA	18---	26	61	tund vegetation of arctc tundra	britton,me	1957
TBOIA	9....	11	74	tund growth forag lich, regulat	andreev,vn	1954

CODEN	VO-NU	BEPA	ENPA	PLCO KEY WORDS----------	AUTHORS----------	YEAR
ECMOA	30--1	1	35	frst phytosoc borea for, gr lak	maycock,pf; curti	1960
ECOLA	42--1	177	180	frst net prim prod, fore & shrb	whittaker,rh	1961
NZFSA	1....	80	115	frst cerv, for, scrubl, n fiord	wardle,j; haywar/	1971

frst continued on the next page

*PLCO = plant community

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
OIKSA	7---2	202	205	frst	estim avrg produc by trees	ovington,jd; pear	1956
XFNCA	63---	1	55	frst	virgn plant communs, minne	ohmann,lr; ream,r	1971

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
ECMOA	22--4	301	330	cofo	forest veg classif, idaho,	daubenmire,r	1952
JWMAA	5---1	90	94	cofo	odvi, mgt sugges, wh-cedar	aldous,se	1941

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
ATRLA	17-15	187	202	defo	food supply, decid, poland	bobek,b; weiner,/	1972
OIKSA	32--3	373	379	defo	brows pressure, decid, eur	bobek,b; perzano/	1979

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
BOREA	16--6	283	360	gras	ecology of the grassland	hanson,hc	1950
CNAPA	876..	1	11	gras	shortgr prair, albert, sas	smoliak,s; peters	1952
ECMOA	8---1	57	114	gras	char maj grassl types, n d	hanson,hc; whitma	1938
ECMOA	20--4	271	315	gras	ecol, mixed prairie, canad	coupland,rt	1950
ECOLA	29--4	449	460	gras	grassl types, s cent monta	wright,jc; wright	1948
JECOA	49--1	135	167	gras	grassl classif, n gt plain	coupland,rt	1961
JRMGA	5---2	84	89	gras	forage prod, n platte isls	ruby,es	1952
JRMGA	7---6	250	255	gras	doca, rnge fora util, oreg	harris,rw	1954
JWMAA	35--2	238	250	gras	anam, food, rng chars, alb	mitchell,gj; smol	1971
JWMAA	42--3	581	590	gras	bibi, diet, slv rivr, nw t	reynolds,hw; han/	1978
OIKSA	10--1	38	49	gras	prim prod in terres commun	bray,jr; lawrenc/	1959

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
AMNAA	97--2	300	320	dsrt	factrs affec seed reserves	nelson,jf; chew,r	1977

dsrt continued on the next page

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS----------	AUTHORS----------	YEAR
JRMGA	20--1	21	25	dsrt	gras, anam, dosh, wyo dese	severson,ke; may,	1967
SWNAA	21--3	311	320	dsrt	standng crop, carb pathwys	syvertsen,jp; ni/	1976

CODEN	VO-NU	BEPA	ENPA	PLCO	KEY WORDS----------	AUTHORS----------	YEAR
AMNAA	31--3	697	743	many	range vegetat, texas, odvi	buechner,hk	1944
ECMOA	21--4	317	378	many	gras, marsh communs, alask	hanson,hc	1951
ECMOA	45--4	389	407	many	odvi, desc dynam plnt comm	grigal,df; ohmann	1975
JECOA	45--2	593	599	many	stand crop nat veg, subarc	pearsall,wh; newb	1957
JRMGA	24--5	346	351	many	herb use of plnt comms, bc	mclean,a; lord,l/	1971
OIKSA	7---2	193	201	many	standng crop natural veget	pearsall,wh; gorh	1956
XAGCA	796--	1	27	many	doca, forag util summ rang	pickford,gd; reid	1948

PLCO = plant community

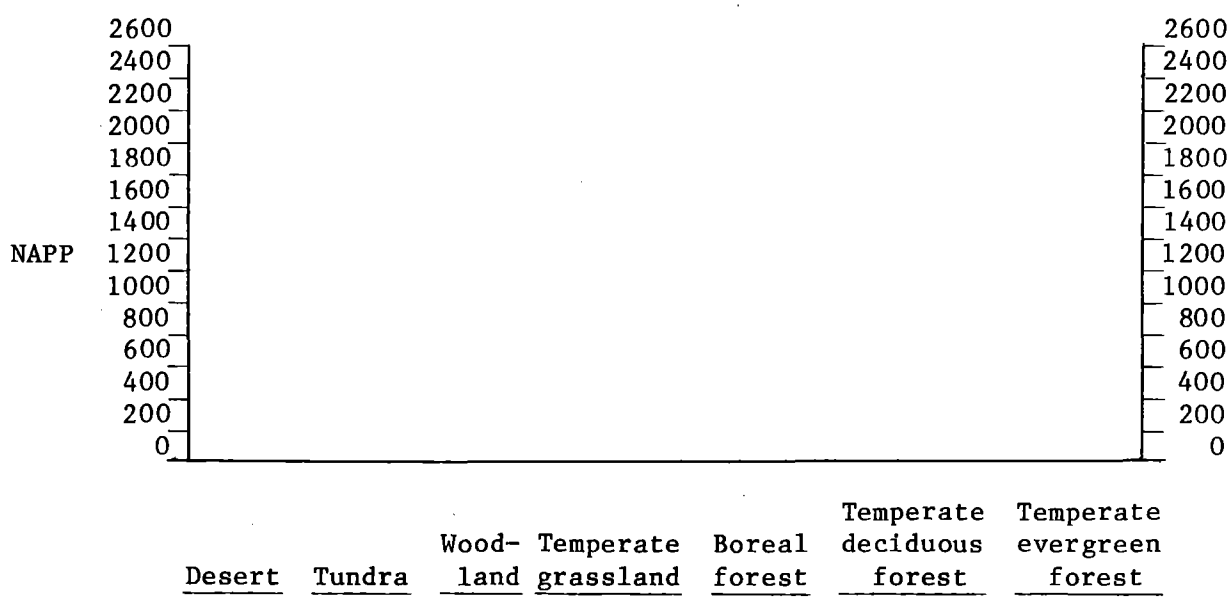
tund = tundra
frst = forest, mixed or unspecified
cofo = coniferous forest
defo = deciduous forest
wdld = woodland
gras = grassland
dsrt = desert
many = more than one community

CHAPTER 13, WORKSHEET 1.1a

Net primary productivities in different vegetation units

Net primary productivity values have been given for several different vegetation types previously in this UNIT. These values will be remembered best by relating them in a way that provides both visual and mental impacts.

Make a bar chart below for the mean and range of net primary productivities in each of the vegetation types, beginning with the lowest and ending with the highest. The values to be plotted are in the table on page 8 of this UNIT. NAPP = net annual productivity in grams/square meter.



The completed bar chart above will provide a visual impression of the quantity of net annual primary productivity. The next WORKSHEET provides an opportunity to visualize the structure of the plant community.

CHAPTER 13, WORKSHEET 1.1b

Visual representations of the vertical structure of plant communities

Each of you have likely had some experience with two or more of the plant communities discussed in this unit. Convert your mental impressions of community structure to drawings in the spaces below, emphasizing the vertical dimension, including overall height and the relative heights of canopies, sub-canopies, shrub layers, and herb layers in each community. HGTM = height in meters.

HGTM

Desert

HGTM

Tundra

HGTM

Woodland

HGTM

Boreal forest

HGTM

Temperate grassland

HGTM

Temperate deciduous forest

HGTM

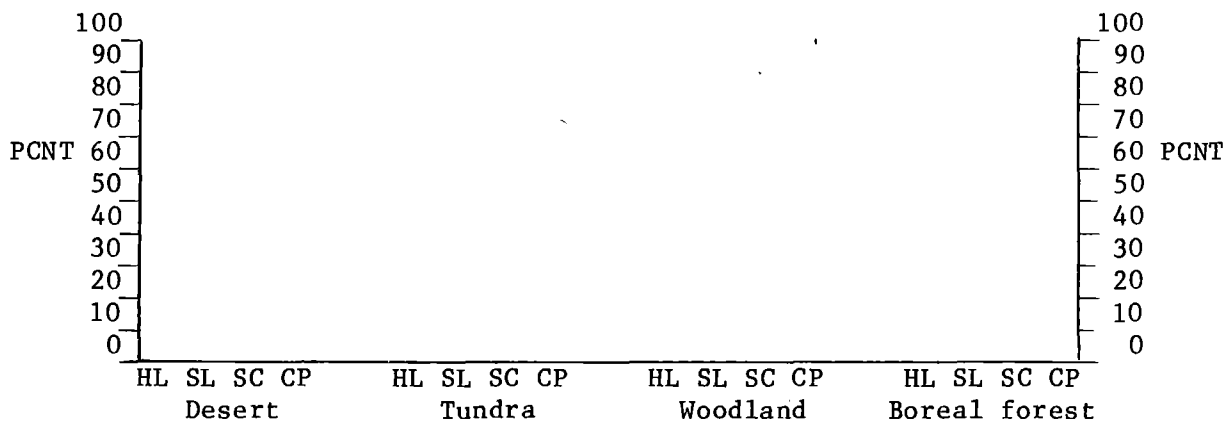
Temperate evergreen forest

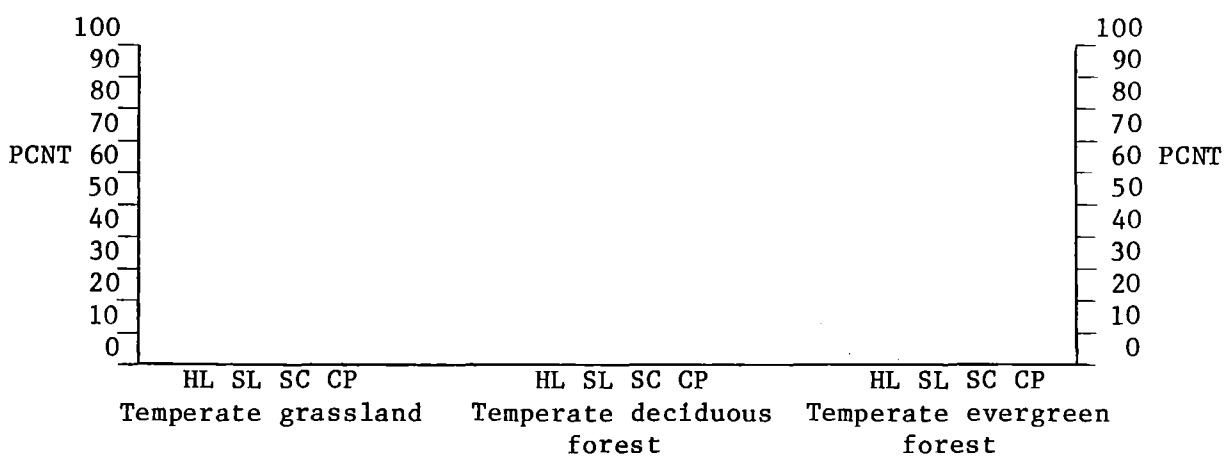
HGTM

CHAPTER 13, WORKSHEET 1.1c

Quantities of primary production in different plant communities

Quantities of primary production in different plant communities were discussed in WORKSHEET 1.1a and the physical structures, i.e. layers, in WORKSHEET 1.1b. Now combine these two into a single drawing, using a bar chart to indicate the relative proportions (PCNT = percent) of the primary productivity found in each of the layers. HL = herb layer, SL = shrub layer, SC = sub-canopy, and CP = canopy.

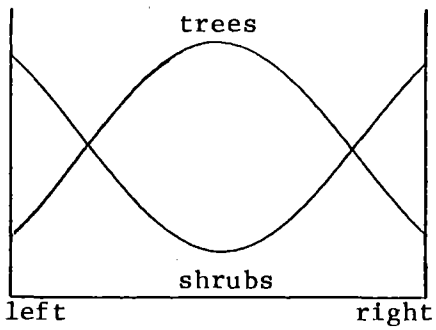




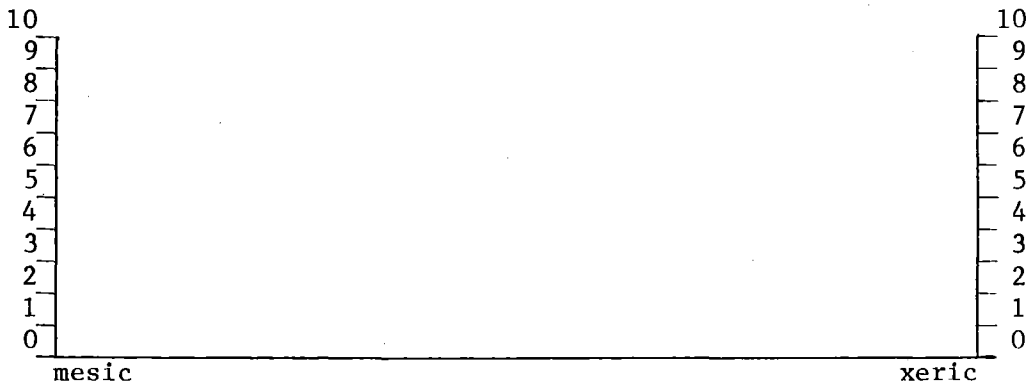
CHAPTER 13, WORKSHEET 1.1d

Primary production in relation to a moisture gradient

Primary production is dependent in part on moisture conditions. Think of the moisture conditions characteristic of each of the plant communities discussed in this UNIT. Now draw the trends in the productivity of each of the strata in relation to a moisture gradient, with the most moist conditions (mesic) on the left and the least (xeric) on the right. After attempting to convert your mental impressions to visual ones, check the drawings in Whittaker and Niering (1975) to see how yours compare. A sample drawing is given to get you started in the kinds of picture being suggested.



Trees increase and then decrease, and shrubs decrease and then increase in relation to left to right.



LITERATURE CITED

Whittaker, R. H. and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. Biomass, production, and diversity along the elevation gradient. Ecology 56(4):771-790.

UNIT 1.2: FORAGE PRODUCTION MEASUREMENTS

The amount of forage produced is a fundamental calculation in the animal requirement: range supply relationship that underlies the concept of carrying capacity. Measurements of forage production are difficult and time-consuming. They are difficult because of problems in sampling and because of very complex (from a statistical point of view) plant population structures. They are time-consuming because the removal of new growth from each plant simply cannot be done quickly. Since wild ruminants forage selectively, clipping of the forage must also be done selectively, if it is to represent the forage of interest to wild ruminants.

Clipping forage is ususlly done on sample plots with areas equal to some convenient proportion to an acre (43560 square feet) or hectare (10000 square meters). Radii and sides of circular and square plots with different areas are tabulated below. A circular plot with a radius of 11.8 feet has an area of 1/100th acre, and if r = 3.6 feet, A = 1/1000th acre. In hectares, a circular plot with a radius of 5.64 meters has an area of 1/100th hectare, if r = 1.78 meters, A = 1/1000th hectare, and if r = 0.56 meters, A = 1/10000th hectare.

one acre = 43560 square feet:

r = 11.8 feet, A = 1/100th acre
s = 20.9 feet, A = 1/100th acre

r = 3.6 feet, A = 1/1000th acre
s = 6.6 feet, A = 1/1000th acre

one hectare = 10000 square meters:

r = 5.64 meters, A = 1/100th hectare
s = 10.00 meters, A = 1/100th hectare

r = 1.78 meters, A = 1/1000th hectare
s = 3.16 meters, A = 1/1000th hectare

r = 0.56 meters, A = 1/10000th hectare
s = 1.00 meters, A = 1/10000th hectare

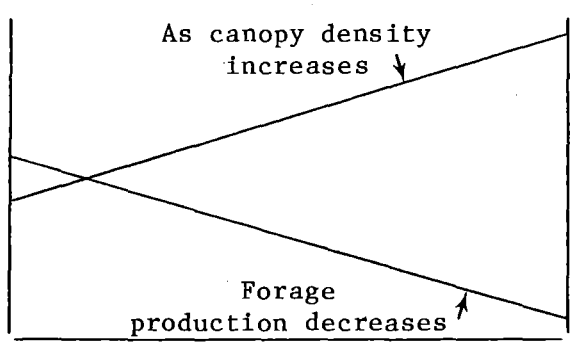
Forage production should also be measured vertically so the distribution of the forage in the foraging space may be evaluated in relation to the heights reached by different species, ages, and sexes of wild ruminants and to the effects of snow accumulation on the forage supply. The vertical distribution of forage production is determined by measuring production at 12-inch or 25-centimeter intervals up to the heights reached by different species of animals.

	250	
	225	100 kg
CM	200	70 kg
	175	40 kg
	150	
	125	
	100	
	75	
	50	
	25	
	0	

Heights reached by white-tailed deer of different weights are indicated on the scale on the left. If snow crusts support the deer, then the height of the crust is added to the height reached.

The amount of forage produced is very much dependent on the canopy characteristics of each plant community. Grasslands and tundra have no canopy above the foraging space of wild ruminants; forage production is equal to primary production. In forest communities, overhead canopy characteristics become very important determinants of the amount of forage produced in the foraging space of wild ruminants as dense canopies filter out sunlight necessary for photosynthesis in the shrub and herb layer. Under some canopies, such as a dense evergreen forest canopy, shrub and herb layers are practically non-existent. A dense deciduous canopy also limits forage production in the understory. Sugar maple stands, for example, have very dense canopies and forage production in the understory is very low, consisting primarily of sugar maple seedlings.

The patterns of forage production in relation to canopy characteristics that may be observed suggest that forage production is predictable from canopy characteristics. The relationship may be illustrated with the two lines below.



The relationship is not this simple in natural habitats, of course, but it is generally true in wild ruminant habitat on the North American continent. The lines representing this relationship should probably not be straight; data in the literature may be plotted in WORKSHEET 1.2a and the shapes of the lines determined.

Canopy characteristics are very much related to the stage in succession, with species composition, canopy density, and canopy depth all important determinants of forage production. Succession effects are discussed in UNIT 1.4, where the basic relationships between plant community characteristics and forage production are discussed further, especially in relation to forest type data.

REFERENCES, UNIT 1.2

FORAGE PRODUCTION MEASUREMENTS

SERIALS

CODEN	VO-NU	BEPA	ENPA	FRGE*KEY WORDS----------	AUTHORS----------	YEAR
CAFGA	34--4	189	207	frge od range surv methods, mgt	dasmann,wp	1948
CAFGA	37--1	43	52	frge deer range survey methods	dasmann,wp	1951
CAFGA	40--3	215	234	frge odhe-fora reln lassen-wash	dasmann,w; blaisd	1954
JWMAA	3---4	295	306	frge yellowst wint rnge studies	grimm,rl	1939
NAWTA	6----	118	126	frge fora inventory meths, biga	schwan,he; swift,	1941

CODEN	VO-NU	BEPA	ENPA	FRGE KEY WORDS----------	AUTHORS----------	YEAR
ATRLA	17-14	171	186	brws meth brows est, dif forest	bobek,b; dzieciol	1972
ECOLA	51--6	1098	1101	brws canop area & vol reln prod	peek,jm	1970
JOMAA	25--2	130	136	brws a deer brwse survey method	aldous,se	1944
JRMGA	14--5	274	278	brws whitesage productn, growth	kinsinger,fe; str	1961
JRMGA	18--4	220	222	brws est brows, twig, stem meas	schuster,jl	1965
JRMGA	19--1	34	38	brws twig diam-length-weight re	basile,jv; hutchi	1966
JWMAA	2---2	131	134	brws carry capac big game range	young,va	1938
JWMAA	19--2	215	225	brws ungu winter browse, idaho	hoskins,lw; dalke	1955
JWMAA	27--3	428	437	brws twig-count meth meas brows	shafer,el,jr	1963
JWMAA	33--2	399	403	brws optim plot samp, est brows	barrett,jp; guthr	1969
JWMAA	33--4	917	921	brws twig wt-diam relat brws sp	telfer,es	1969
JWMAA	34--2	456	460	brws lgth-, wt-dia rel, serv-be	lyon,lj	1970
JWMAA	35--3	501	507	brws var twig diam-wt rel, minn	peek,jm; kreftin/	1971
PCGFA	21---	57	62	brws grwth & forag quali, 4 spp	blair,rm; halls,l	1967
VILTA	9---3	45	192	brws wiru, win habita, land use	ahlen,i	1975
XAFNB	66---	1	4	brws prod, rapid sampl, computr	stearns,rw; schw/	1968
XANEA	33---	1	37	brws odvi browsng hrdwd, northe	shafer,el,jr	1965
XANEA	100--	1	25	brws design, anal studies brows	shafer,el,jr; lis	1968

CODEN	VO-NU	BEPA	ENPA	FRGE KEY WORDS----------	AUTHORS----------	YEAR
XFNSA	23---	1	5	twig seas twg grwth so brws spp	hall,lk; alcaniz,	1965

*FRGE = forage type

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
AGJOA	41--2	63	65	hrbg	tech est prod, rnge, pastu	frischknecht,nc;/	1949
AGJOA	50--9	504	506	hrbg	plnt ht x cover estim prod	evans,ra; jones,m	1958
JDSCA	28--3	171	185	hrbg	samplng proced, pastur yld	nevens,wb	1945
JRMGA	2---1	30	32	hrbg	determ forag weight, south	cambell,rs; cassa	1949
JRMGA	4---4	270	278	hrbg	aer phot, sub-sam, rng inv	harris,rw	1951

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
UTSCB	29--1	3	6	forb	anam, seas forage use, uta	beale,dm; scotter	1968

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ATICA	21--4	255	259	lich	growth rate lichen, alaska	pegau,re	1968

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
FOSCA	2....	314	320		spherical densiometer, est	lemon,pe	1956
FPWTA	25...	5	16		study woodl cari rang, ont	ahti,t; hepburn,r	1961
NOSCA	33--1	43	64		canopy-cov meth, veg analy	daubenmire,r	1959

FRGE = forage type

frge = mixed or unspecified forage types
brws = browse
twig = twigs
hrbg = herbage or herbaceous vegetation
forb = forbs
lich = lichens

UNIT 1.3: SPATIAL DISTRIBUTION OF FORAGE PRODUCED

Spatial distributions of forage produced involves three dimensions, including x and y for the horizontal plane and z for the vertical dimension. Distribution over land areas (the horizontal plane) have been studied in many places with both direct and indirect measurements. Forage production values, expressed as pounds per acre or kg per hectare, are available for given areas, usually with reference to the kind of vegetation. Vertical distributions of forage production are almost entirely unknown; measurements of this important characteristic of the range simply have not been made. Measurements on vertical strata make collections more time-consuming, but the effort should be made for different plant communities so the different possible shapes of vertical profiles could be identified. Vertical profiles are important because animals of different species, ages, and sexes can reach to different heights, and snow covers up forage, making less available to animals in the winter. In fact, large amounts of forage may be concentrated in seedlings near the ground surface, and a covering of snow could make a considerable part of that forage supply unavailable. This is an important consideration in the winter when nutritional stress may be great, especially for the younger and smaller animals who not only cannot reach as high for forage as larger animals, but also have greater difficulty in moving through snow.

A major factor affecting the amount of forage produced that is within reach of the wild ruminant is the density of the canopy. Dense forest canopies intercept a high fraction of the sunlight, allowing little to reach the shrub layer. Deer browse production under a dense forest canopy is less than 25 pounds per acre per year (Severinghaus 1973), which is less than 3 gms per square meter, a very small quantity indeed! This amount of forage produced is especially small when compared to primary production, which may be several hundred gms/square meter, nearly all of it in the canopy. Forage production may reach a thousand pounds or more, with the largest production in those areas with the best growing conditions, i.e. good soil, adequate water, and temperature and light conditions that promote high levels of photosynthesis.

A significant conclusion was reached by Telfer (1972) who compared measured forage yield in New Brunswick and Nova Scotia with values reported in other studies. From the highlight (page 446):

> "Forage yields per acre were comparable to values reported from many studies in western North America, but plant composition differed."

This conclusion is significant because it suggests that the same kind of plant community structure results in similar values of forage production. The species in the plant communities are not as important as the forest type, which means that forest type data, which is readily available for many forested areas, may be used to estimate expected forage production. If this is possible and the vertical distribution patterns of forage in different forest types are known, then the amount of forage in all three dimensions of the foraging space can be estimated and used in relation to changing range conditions and population characteristics.

It is important to point out here that the general patterns are most important as the effects of differences and changes are evaluated in relation to the ruminant populations. Once these patterns have been recognized and the mechanisms for evaluating differences and changes determined, then local conditions can be measured and evaluated since the procedures for evaluating the relationships will not change, only the numbers will.

VERTICAL DISTRIBUTIONS

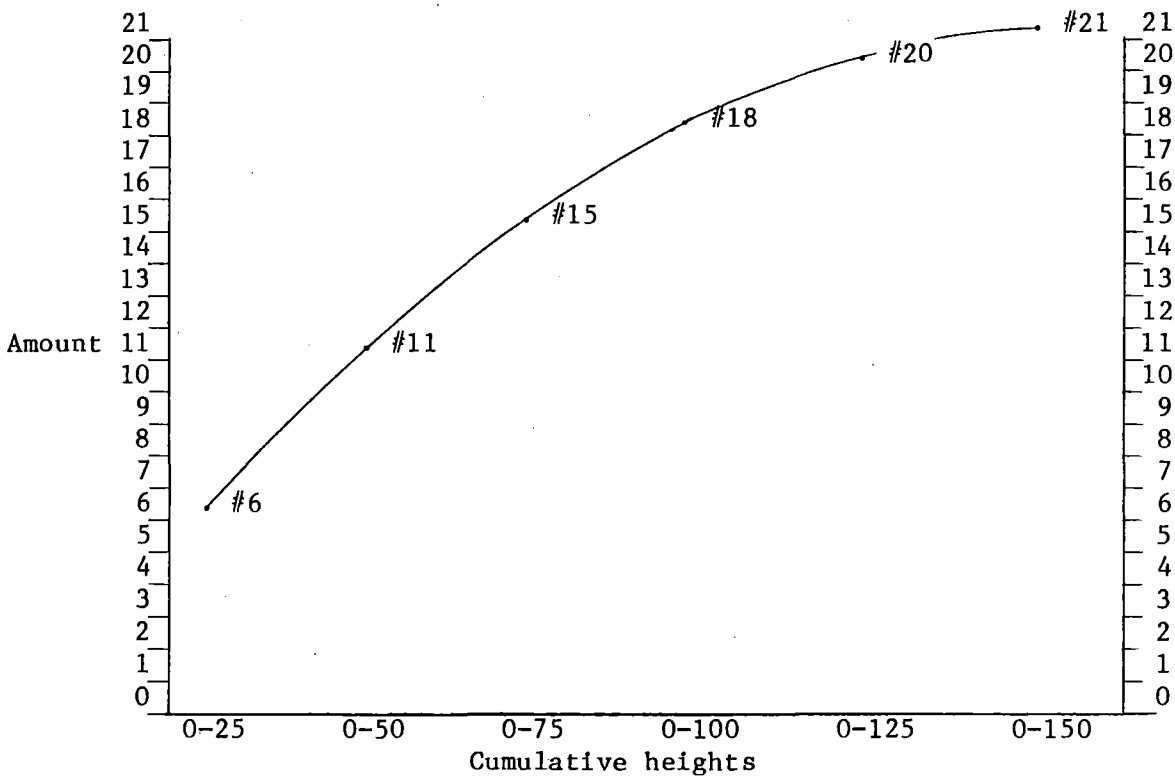
The vertical distribution of forage production, a characteristic of the habitat that has been given practically no attention, may be described quantitatively in two different ways. The illustration below shows the amounts present (X = one unit) at each height interval, representing the results measured in each stratum. This vertical distribution shows the largest quantity in the lowest height interval and the smallest in the highest height interval.

Amount	0-25	25-50	50-75	75-100	100-125	125-150
6	X					
5	X	X				
4	X	X	X			
3	X	X	X	X		
2	X	X	X	X	X	
1	X	X	X	X	X	X
0	X	X	X	X	X	X

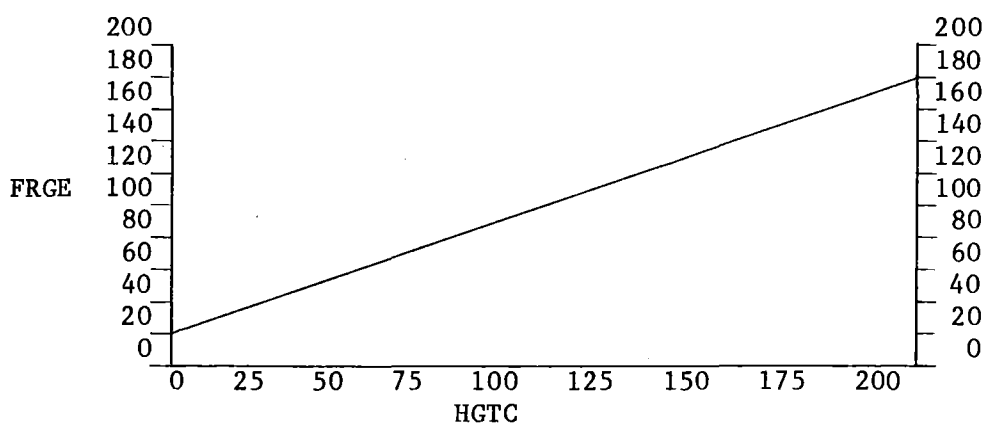
Height intervals

The above chart illustrates the amount present (X = one unit) in each interval, but it does not illustrate how much is present in the total foraging space.

The drawing on the next page represents the cumulative amount from the first height interval of 0-25 through the cumulative height of 0-150 cm. The amount up to any height is clearly indicated in the line drawing.



Cumulative amounts of forage in relation to cumulative heights may be expressed with equations and used to estimate not only the amount of forage up to any height, but also the amount between height intervals. The drawing below illustrates these calculations.



The equation for the line drawn above is:

$$FRGE = 20 + 0.8\ HGTC,$$

where FRGE = kg/hectare and
HGTC = height in cm.

The amount of forage available to an animal that can reach 180 cm is 20 + 0.8 (180) = 164 kg/hectare. Suppose that snow covered the lower 50 cm of vegetation. The amount of forage available to this animal may be calculated by determining the forage available up to the height reached and subtracting the amount covered by snow. Thus:

$$\left[20 + 0.8\ (180)\right] - \left[20 + 0.8\ (50)\right] = 104 \text{ kg/hectare.}$$

These illustrations show how vertical distributions can be used and why they can be important. Actual distributions of forage may make considerable difference to animals of different sizes, especially in winter when nutritional stress may be severe. Some actual measurements are included in WORKSHEETS, and additional evaluations of the effects of vertical distributions are made in CHAPTERS 17 and 20.

LITERATURE CITED

Severinghaus, C. W. 1973. A modest proposal to improve deer habitat. The Conservationist 27(6):37.

Telfer, E. S. 1972. Forage yield in two forest zones of New Brunswick and Nova Scotia. J. Range Manage. 25(6):446-449.

REFERENCES, UNIT 1.3

SPATIAL DISTRIBUTION OF FORAGE PRODUCED

SERIALS

CODEN	VO-NU	BEPA	ENPA	FRGE*KEY WORDS----------	AUTHORS----------	YEAR
JFUSA	65-11	807	813	frge forest cover and logging	young,ja; hedric/	1967
JRMGA	25--6	446	449	frge yld, 2 for zon, n b, nov s	telfer,es	1972
PSAFA	1962-	165	167	frge timb ovrstry detrm od fora	schuster,jl; hall	1962
RWLBA	9---1	1	146	frge edge eff, lesser veg, adir	barick,fb	1950
XFPNA	112--	1	12	frge seas forag use, elk & deer	edgerton,pj; smit	1971
XFWWA	43...	1	48	frge rata st matthw islan range	klein,dr	1959
ZHIVA	11...	62	68	frge rata fodder supply, zhivot	ustinov,vi; pokro	1954

*FRGE = forage type

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
CNSVA	27--6	37	37	brws	propos to imprv od habitat	severinghaus,cw	1973
JWMAA	5---1	90	94	brws	mgt sugges for wh-cedr typ	aldous,se	1941
JWMAA	23--3	273	278	brws	odvi win rng veg stud, wis	habeck,jr	1959
JWMAA	35--3	533	537	brws	wldlf food, hrdwd, reg cut	crawford,hs,jr; /	1971
JWMAA	40--2	326	329	brws	odvi brwse inventor, louis	pearson,ha; stern	1976
MXSBA	294--	1	43	brws	isl roy forst, wldlf, fire	hansen,hl· kreft/	1973
NAWTA	18---	581	596	brws	od yard carry cap, browsng	davenport,la; sw/	1953
NFGJA	14--2	193	198	brws	witchhob, site exp, brwsng	bailey,ja	1967
PCGFA	9----	134	156	brws	brow cens, 100 % clip meth	harlow,rf	1955
VILTA	9---3	45	192	brws	wiru, win habita, land use	ahlen,i	1975
WLSBA	6---4	259	260	brws	age, densi, fert, oak prod	wolgast,lj	1978
XFNSA	140--	1	4	brws	odvi browse resourc, arkan	segelquist,ca; p/	1972
XFSEA	2----	1	20	brws	od browse resourc, n georg	ripley,th; mcclur	1963

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
JWMAA	32--1	185	186	twig	brows yield, forst opening	halls,lk; alcaniz	1968

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ECOLA	27--3	195	204	hrbg	graz val natv veg, so pine	campbell,rs	1946
ECOLA	35--1	59	62	hrbg	for prod, longlf pne, alab	gaines,em; campb/	1954
JECOA	45--2	593	599	hrbg	stand crop nat veg, subarc	pearsall,wh; newb	1957
JFUSA	63--4	282	283	hrbg	tree - herbage relations	hall,lk; schuster	1965
JRMGA	5---2	76	80	hrbg	herb, ungu, wint-rang util	buechner,hk	1952
JRMGA	26--6	423	426	hrbg	s pine overstory infl herb	wolters,gl	1973
PSAFA	1957-	156	158	hrbg	undrstory veg, stand chars	pase,cp; hurd,rm	1957

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ECOLA	50--5	802	804	leav	foliage profile, vert meas	macarthur,rh; hor	1969

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
JFUSA	48--2	118	126	gras	chng pond pne bnchgras rng	arnold,jf	1950

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ASZBA	16--2	155	161	lich	prod arboreal lichns, rata	scotter,gw	1961

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ECMOA	35...	259	284		ecolog, deer range, alaska	klein,dr	1965
JFUSA	46--6	416	425		util summ range plnts, uta	cook,cj; cook,cw/	1948
JWMAA	32--2	330	337		odvi food ylds, 4 for typs	segelquist,ca; gr	1968
JWMAA	42--4	799	810		ceel diet, actv, ldgpl pne	collins,wb; urne/	1978
WMBAA	18---	1	111		effs wldfre rata wint rnge	scotter,gw	1964

FRGE = forage type

frge = mixed or unspecified forage types
brws = browse
twig = twigs
hrbg = herbage or herbaceous vegetation
leav = leaves
gras = grasses
lich = lichens

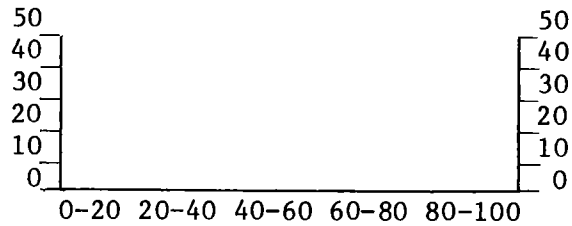
CHAPTER 13, WORKSHEET 1.3a

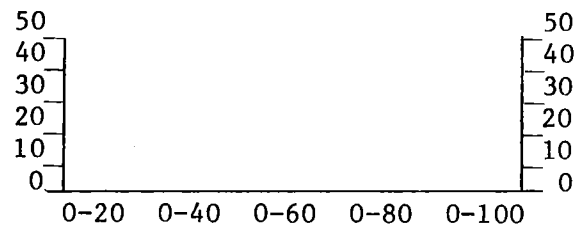
Vertical distributions of forage

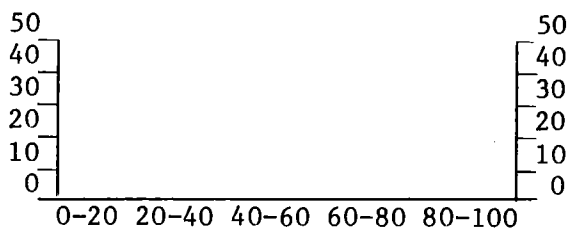
Draw possible vertical distributions of forage in different plant communities in the spaces below and on the next page, putting the interval data on the left and cumulative data on the right. Make up different patterns of interval data based on different plant community structures discussed in UNIT 1.1. See how different interval distributions affect the cumulative distributions.

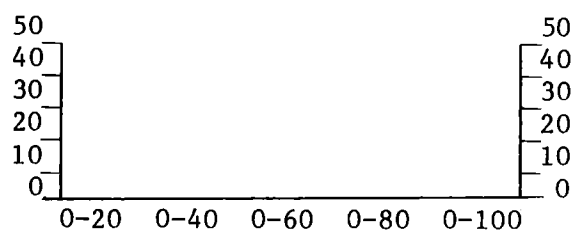
Interval data

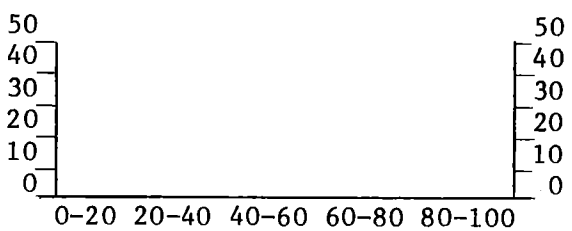
Cumulative data

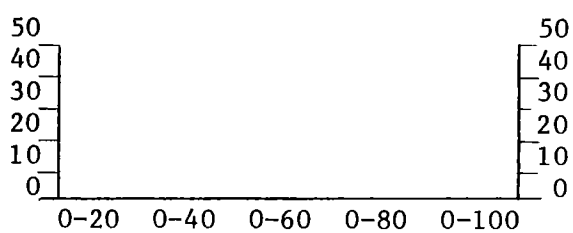


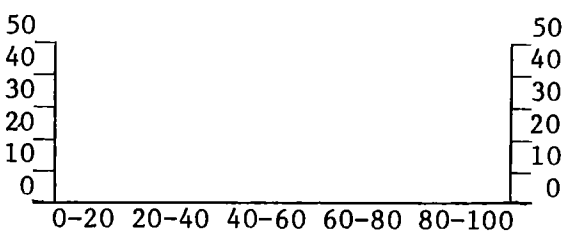


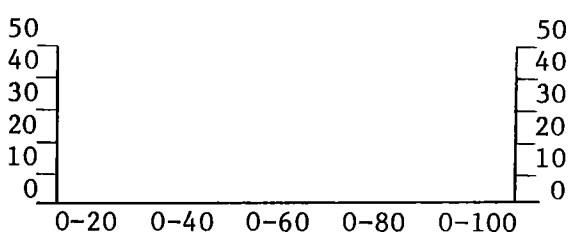




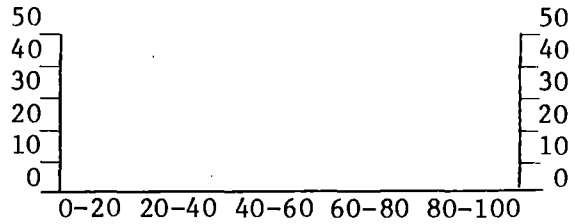


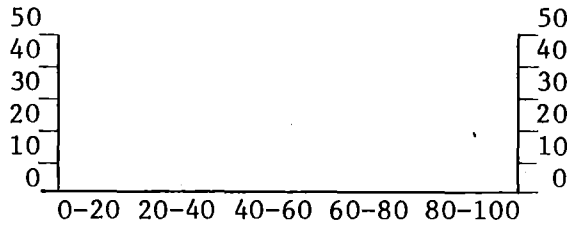


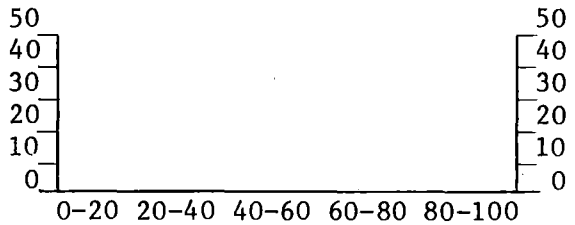


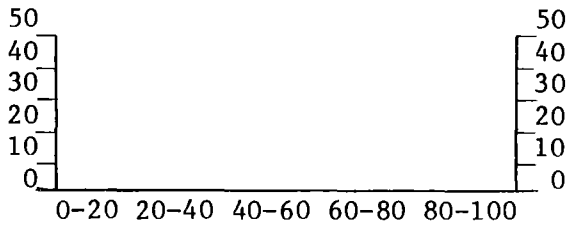


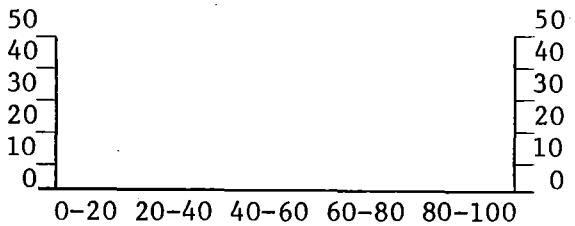
Interval data Cumulative data

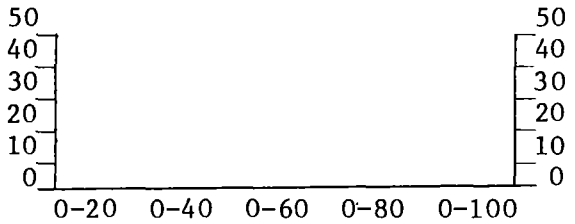


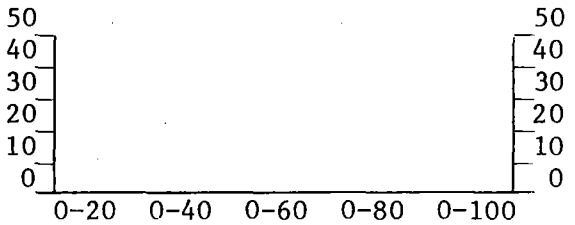


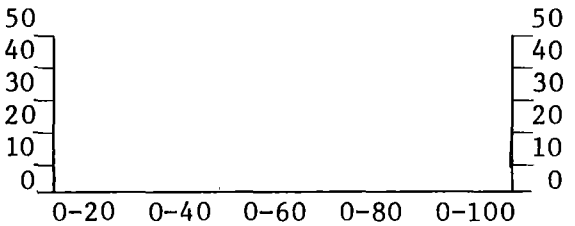


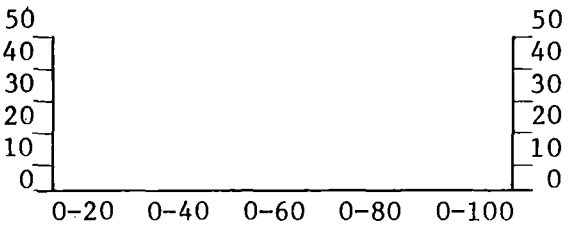


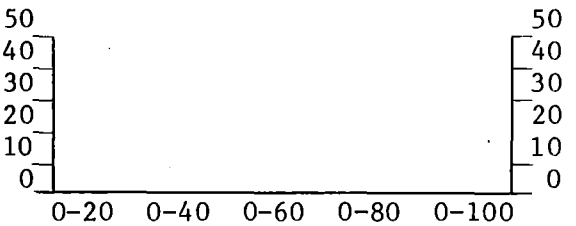












CHAPTER 13, WORKSHEET 1.3b

Measured vertical distributions of forage

Measurements of forage production at 25 cm vertical intervals in three deciduous stands near Ithaca, New York show differences in forage production between stands but similar patterns of distribution of the forage in these stands. The cumulative sums of forage quantities are close to straight lines, so linear regression equations may be used to calculate the weights of forage up to any height.

Stand descriptions and equations are, where WFKH = weight of forage in kg/hectare and HGTC = height in centimeters:

McGowan's Woods; 70 year-old mixed hardwood stand:

$$WFKH = 2.2926 + 0.03942\ HGTC; \quad R^2 = 0.995$$

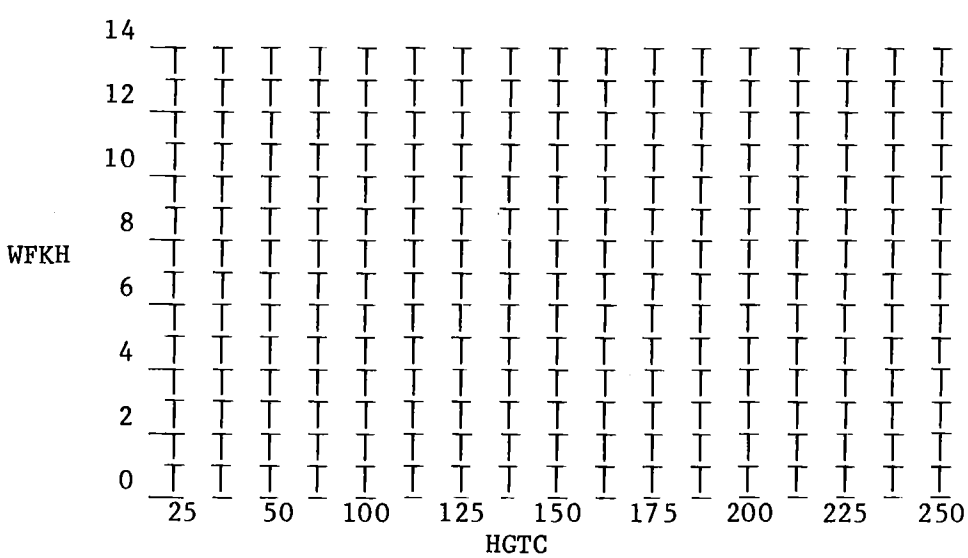
Turkey Hill; 55 year-old mixed hardwood stand, primarily oak and maple:

$$WFKH = 5.0174 + 0.03499\ HGTC; \quad R^2 = 0.942$$

Arnot Forest; 35 year-old sugar maple stand:

$$WFKH = 0.69147 + 0.00679\ HGTC; \quad R^2 = 0.0946$$

Plot and label the lines on the grid below. Note that the sugar maple stand, which had a dense canopy, had much less forage than did the two mixed hardwood stands.



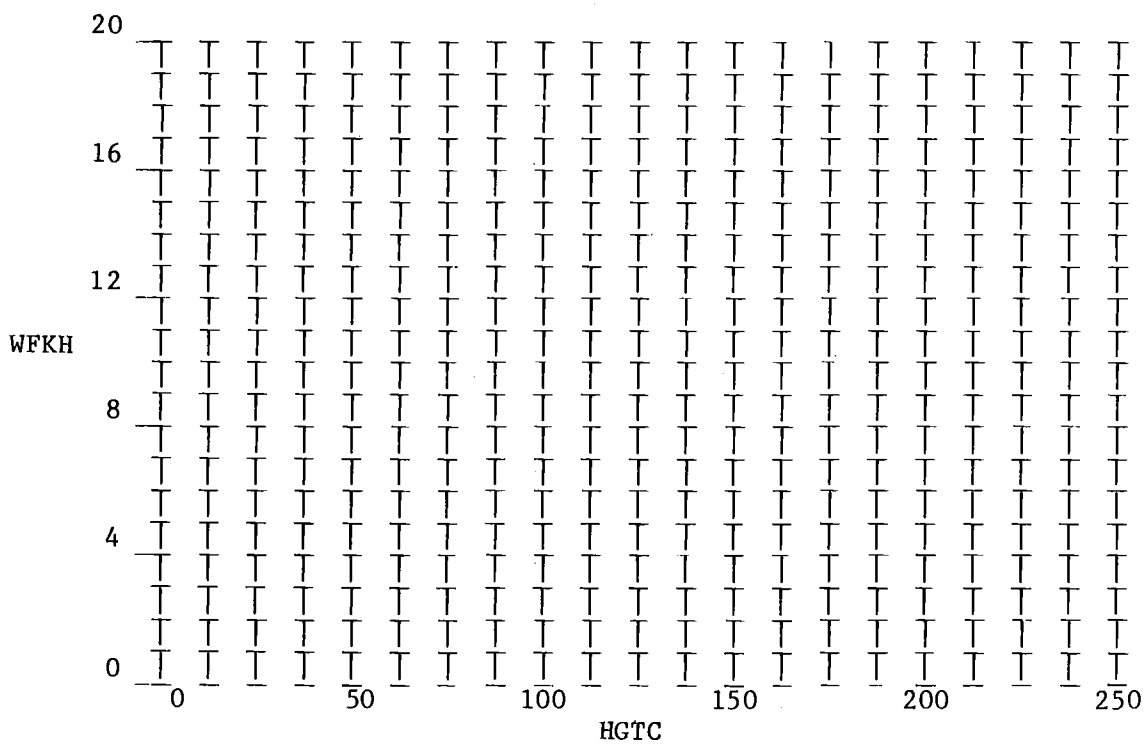
CHAPTER 13, WORKSHEET 1.3c

Equations for predicting vertical distributions of forage production

The array of equations below illustrates the effects of different values of a and b on the distribution of forage. Higher values of a indicate greater quantities of forage in the first 25 cm, and higher b values indicate greater quantities per unit height.

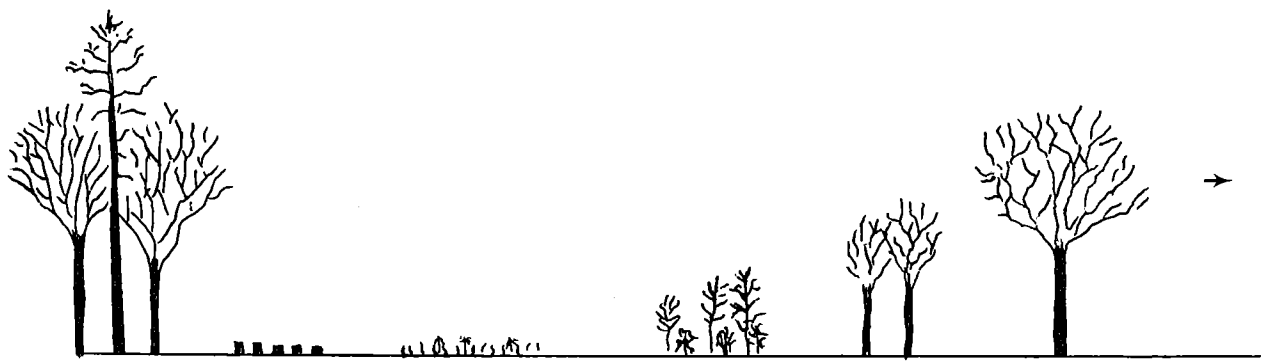
The different distributions may be used to illustrate the effects of snow depths on forage resources available.

Equation number	
1.	WFKH = 7.78 + (0.048) HGTC
2.	WFKH = 6.00 + (0.040) HGTC
3.	WFKH = 4.22 + (0.031) HGTC
4.	WFKH = 2.22 + (0.031) HGTC
5.	WFKH = 0.22 + (0.031) HGTC
6.	WFKH = 4.89 + (0.004) HGTC
7.	WFKH = 2.89 + (0.004) HGTC
8.	WFKH = 0.89 + (0.004) HGTC



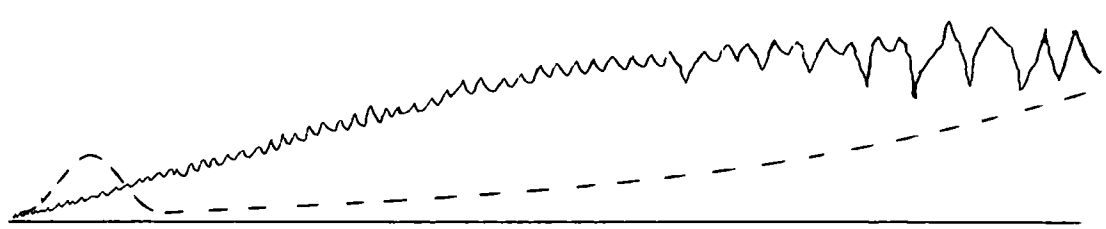
UNIT 1.4: FORAGE PRODUCTION AT DIFFERENT STAGES OF SUCCESSION

The stage in succession is a very important determinant of the amount of forage produced. Early stages in succession may result in 400 pounds of browse per acre (Severinghaus 1974), and over 1000 pounds of browse and other forage have been measured in recent field work at Cornell's Wildlife Ecology Laboratory. More mature stages are characterized by dense canopies and little forage production in the understory; less than 25 lbs of deer browse per acre will be produced under a closed canopy. Logging and fire open the canopy, allowing light to reach the forest floor and stimulate new growth, resulting in increased amounts of forage production in the early stages of secondary succession. As succession continues, the canopy closes and forage production is reduced again. This predictable sequence is illustrated in the sketch below.



Crown closed	Logging or fire	Grasses & annual herbs	Seedlings and shrubs	Saplings	Mature trees	Crown closed again

If secondary succession proceeds without logging or fire to a point where the climax forest contains overmature trees that are subject to blowdown, decline in vigor, and eventual death, then the later stages in succession will show a rise in forage production. Wallmo and Schoen (1980) illustrate this for the temperate coniferous rain forest in Southeast Alaska. There, fire is uncommon and logging has resulted in an array of even-aged stands of various ages. Overmature stands are also present. These conditions result in openings in the canopy and a rise in the forage production curve to the right of the one sketched above from Severinghaus. Over a longer time scale, the forage production pattern looks like this:



Overmature stands are not abundant in many areas of North America. Short cutting rotations for pulpwood and firewood, for example, remove trees early in secondary succession. In wilderness areas and other lands where logging is prohibited, the potential for overmature and more open canopies late in succession exists. Such areas should be left subject to fires at natural time intervals.

The forage production patterns illustrated by both Severinghaus (1974) and Wallmo and Schoen (1980) are predictable enough to use when making estimates of forage production in relation to forest type. Using the basic pattern in relation to the stage in succession and making some adjustments in absolute quantities in relation to growing conditions and perhaps species composition, forage production estimates may be made and related to forage consumption discussed in CHAPTER 12. Forage consumption by individuals is dependent on their size, reproductive rate, and ecological metabolism (CHAPTERS 1, 18, and 7, respectively) and forage consumption by the population is dependent on the metabolic structure of the population (CHAPTER 19). Thus the basic parameters in the energetic framework of animal-range relationships have been identified and represented by equations so quantitative evaluation may be completed.

LITERATURE CITED

Severinghaus, C. W. 1974. Return of the deer. The Conservationist 29(1):39-480.

Wallmo, O. C. and J. W. Schoen. 1980. Response of deer to secondary forest succession in Southeast Alaska. Forest Sci. 26(3):448-462.

REFERENCES, UNIT 1.4

FORAGE PRODUCTION AT DIFFERENT STAGES OF SUCCESSION

SERIALS

CODEN	VO-NU	BEPA	ENPA	FRGE	*KEY WORDS----------	AUTHORS----------	YEAR
CNSVA	29--1	39	48	frge	return of the deer	severinghaus,cw	1974
FOSCA	26--3	448	462	frge	resp deer sec succ, alaska	wallmo,oc; schoen	1980

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
CNRDA	28--5	249	271	brws	alal, successn, quan, nutr	cowan,im; hoar,w/	1950

brws continued on the next page

*FRGE = forage type

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
JFUSA	48-10	675	678	brws	deer in reln plnt successn	leopold,as	1950
JFUSA	56--6	416	421	brws	od brws prod fr felled tre	stoeckeler,jh; k/	1958
NAWTA	15---	571	578	brws	deer in reln plnt successn	leopold,as	1950

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ECOLA	41--1	34	49	gras	orgnc produc, old fld succ	odum,ep	1960

CODEN	VO-NU	BEPA	ENPA	FRGE	KEY WORDS----------	AUTHORS----------	YEAR
ECMOA	24--4	349	376		ecol successi abandon farm	beckwith,sl	1954
FRCRA	29--3	218	232		survey, conif fores, rocki	cormack,rgh	1953
WMBAA	18---	1	111		effs wldfre rata wint rnge	scotter,gw	1964

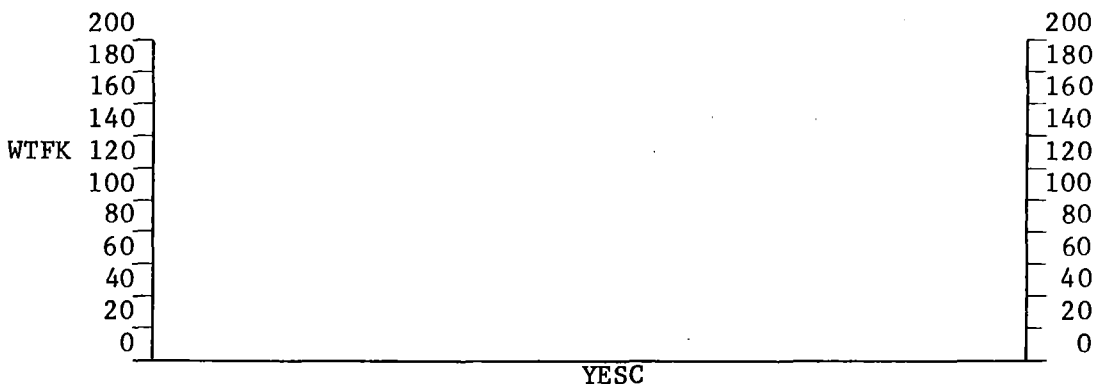
FRGE = forage type

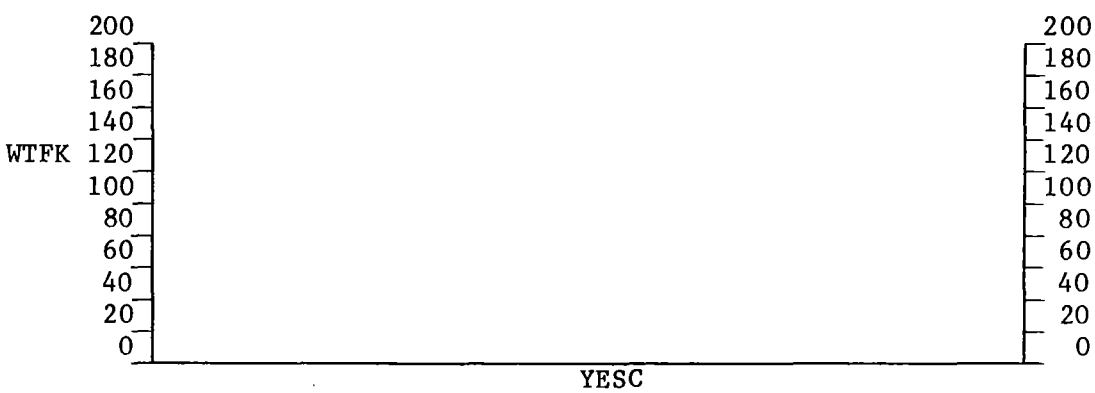
frge = mixed or unspecified forage type
brws = browse
gras = grass

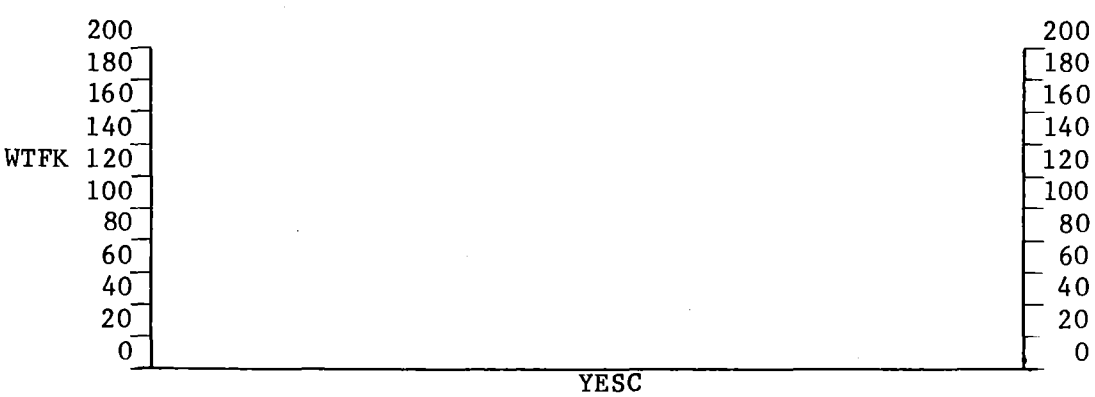
CHAPTER 13, WORKSHEET 1.4a

Weights of forage in relation to years of succession

Patterns of forage production in relation to time and stages in succession have been presented and discussed in this UNIT. Pictures are interesting to look at, but they do not communicate directly with electronic computing equipment. Sketch variations in the weights of forage (in kg) produced in relation to year of succession (YESC) and seek ways to express these variations with equations. Polynomial regressions may be appropriate.







If curve-fitting programs are not readily available, the information shown on the previous page may be tabulated in the column below. Select intervals of YESC (3 years, 5 years, 9 years, or whatever is appropriate for your purposes) and list the expected average forage production for that interval in the blanks below.

Interval of YESC	WTFK
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UNIT 1.5: SEED AND MAST PRODUCTION

Mast production may be an important factor in the diet of some of the wild ruminants. The white-tailed deer, abundant in the eastern deciduous forests, is most affected by acorn production, and separate equations for calculating live weight: field dressed weights for "normal" and "acorn" years are given in CHAPTER 1, WORKSHEET 1.5a, Page 26a.

Seed and mast production is quite varible from year to year, depending on weather conditions in the spring during pollination and through the rest of the growing season. Low temperatures in the spring have a detrimental effect on seed production.

The potential production of seeds and mast is dependent on the density of the seed-producing plants and their sizes. Potential acorn production, for example, is partly dependent on the age and size of the tree. Younger and older trees may have less production than those in the middle range of size and age (Gysel 1956). Gysel cited earlier authors who concluded that variations in seed production, probably due to hereditary differences, almost completely obscured variation due to tree size and growth rate.

Crown expanse is apparently an important factor in the production of acorns. If weather conditions are right for high production, then the open-grown trees with the genetic potential for high production can be expected to be the heaviest producers.

Most measurements of seed and mast production are direct counts each year for sample plots. It would be convenient if production coud be predicted on the basis of tree size and crown characteristics, but variations between individuals within years and in the level of production between years make predictions difficult in some areas.

Expected yields of acorns in relation to bole diameters and crown radius have been calculated with regression equations by Goodrum et al. (1971). The correlation coefficients were quite high (0.69 to 0.97 total range), and the authors suggest that expected yield tables could be used to determine the number of trees required to fulfill the needs of game species. They noted that some trees were inherently poor producers; genetics appear to be very important in determining acorn productivity.

LITERATURE CITED

Goodrum, P. D., V. H. Reid, and C. E. Boyd. 1971. Acorn yields, characteristics, and management criterion of oaks of wildlife. J. Wildl. Manage. 35(3):520-532.

Gysel, L. W. 1956. Measurement of acorn crops. Forest Science 2(4):305-313.

REFERENCES, UNIT 1.5

SEED AND MAST PRODUCTION

SERIALS

CODEN	VO-NU	BEPA	ENPA	TYPE*	KEY WORDS----------	AUTHORS----------	YEAR
JFUSA	61--9	679	680	mast	compare 8 types mast traps	thompson,rl; mcgi	1963
JWMAA	6---2	118	121	mast	yld, persis wildl foo plnt	park,bc	1942
JWMAA	16--3	338	343	mast	meth eval annual mast indx	uhlig,hg; wilson,	1952
JWMAA	17--3	378	380	mast	yield seed, mast, hardwood	dalke,pd	1953
JWMAA	42--3	606	613	mast	fruit prod pne plan, georg	johnson,as; lande	1978
PCGFA	9----	55	60	mast	eff burn forag & mast prod	lay,dw	1955

CODEN	VO-NU	BEPA	ENPA	TYPE	KEY WORDS----------	AUTHORS----------	YEAR
AJBOA	65--4	487	489	acrn	acorn prod, eff site qual,	wolgast,lj	1978
BJASA	23...	21	25	acrn	var in prod of immat acorn	wolgast,lj	1978
FOSCA	2---4	305	313	acrn	measurement of acorn crops	gysel,lw	1956
JFUSA	32--9	1014	1016	acrn	productn, chestnut oak, nj	wood,om	1934
JFUSA	41-12	915	916	acrn	better acrns fr fertlz oak	detwiler,sb	1943
JFUSA	42-12	913	920	acrn	seed prod s appalachi oaks	downs,aa; mcquilk	1944
JFUSA	53--6	439	441	acrn	yld of seed by oak, ozarks	christisen,dm	1955
JWMAA	4---4	404	428	acrn	utili oaks, birds, mammals	van dersal,wr	1940
JWMAA	12--3	227	231	acrn	yld, us, wat & willow oaks	cypert,e; webster	1948
JWMAA	15--3	332	333	acrn	yld fr a post oak, missour	christisen,dm	1951
JWMAA	17--3	380	382	acrn	production in east texas	petrides,ga; par/	1953
JWMAA	35--3	520	532	acrn	acorn yield, charac, manag	goodrum,pd, reid/	1971
JWMAA	41--2	218	225	acrn	pin oak acorn prod, missou	mcquilkin,ra; mus	1977
JWMAA	41--4	685	691	acrn	oak repr, eff age, densty,	wolgast,lj stout	1977
LUFPA	6----	1	43	acrn	factr infl yiel, use acorn	reid,vh; goodrum,	1957
MOARA	750--	1	24	acrn	pin oak acrn prod & regene	minckler,ls; mcde	1960
MOARA	898--	1	15	acrn	pin oak prod, norm & flood	minckler,ls; jane	1965
NAWTA	20---	337	357	acrn	acorn yield, useage, misso	christisen,dm; ko	1955
NIRKA	57...	209	214	acrn	prod, disper, germin acorn	kanazawa,y	1975

*TYPE = type of mast

CODEN	VO-NU	BEPA	ENPA	TYPE	KEY WORDS----------	AUTHORS----------	YEAR
PAABA	635-- 1	22		acrn	evaluat mast yield in oaks	sharp,wm	1958
PCGFA	13--- 54	61		acrn	acorns in diet of wildlife	goodrum,pd	1959
PCGFA	30--- 656	659		acrn	fertil oak stimu mast prod	colvin,tr	1976
PSAFA	1957- 141	147		acrn	eff hardwd remov on wildlf	reid,vh; goodrum,	1957
XFPSA	136-- 1	11		acrn	odvi habi, pine-hardwd, la	blair,rm; brunett	1977
YAXAA	1949- 571	573		acrn	trees and food from acorns	downs,aa	1949

CODEN	VO-NU	BEPA	ENPA	TYPE	KEY WORDS----------	AUTHORS----------	YEAR
JWMAA	11--2 184	185		nuts	method of measuring yields	allen,dl; mcginle	1947
JWMAA	35--3 516	519		nuts	analys beechnut prod & use	gysel,lw	1971

CODEN	VO-NU	BEPA	ENPA	TYPE	KEY WORDS----------	AUTHORS----------	YEAR
JWMAA	29--3 497	503		frui	frui-prod tree, shrb, ozar	murphy,da; ehrenr	1965
JWMAA	32--1 185	186		frui	brws plts yld best in open	halls,lk	1968
JWMAA	35--3 533	537		frui	wldlf food, hrdwd, reg cut	crawford,hs,jr; /	1971
PCGFA	15--- 30	37		frui	fruit prod, undrstry hardw	lay,dw	1961
PCGFA	18--- 57	62		frui	importn variet, south odvi	lay,dw	1964

TYPE = type of mast

mast = more than one or unspecified type of mast
acrn = acorns
nuts = nuts
frui = fruit