Great Basin Naturalist 58(4), © 1998, pp. 312–327

RESPONSE OF UNDERSTORY SPECIES TO CHANGES IN PONDEROSA PINE STOCKING LEVELS IN THE BLACK HILLS

Daniel W. Uresk[1] and Kieth E. Severson[1]

ABSTRACT.—The objective of this study was to test the hypothesis that there are no differences in understory production, by species, due to stocking levels of *Pinus ponderosa* (ponderosa pine). Understory production was estimated, by species, on 3 replicates each of 8 growing stock levels, ranging from clearcuts to unthinned stands, in both sapling- and pole-sized pine stands (48 plots) over 3 nonconsecutive years. All stands were approximately 70 yr old when thinning treatments were applied. Production of many herbaceous species, especially *Agropyron* spp. (wheatgrasses) and *Carex* spp. (sedges), declined as growing stock levels (measured in terms of basal area) of ponderosa pine increased. While trends in total production were similar, there were specific differences between sapling and pole stands. Sedges and *Oryzopsis asperfolia* (roughleaf ricegrass) produced more in sapling stands, whereas *Danthonia intermedia* (timber oatgrass) was more abundant in pole stands. Shrub production, dominated by *Arctostaphylos uva-ursi* (bearberry), was relatively consistent across all stocking levels except unthinned. Although the total number of species declined as pine basal area increased, a few species, such as *Linnaea borealis* (twinflower) and *Shepherdia canadensis* (buffaloberry), were found only under relatively dense pine canopies. While floristic species richness was greater at lower stocking levels of ponderosa pine, the total number of species would be greater if all stocking levels were present.

Key words: understory, ponderosa pine, Black Hills, plant species, biomass, production, stocking levels, floristic diversity.

Understory-overstory relationships have been studied extensively in *Pinus ponderosa* (ponderosa pine) stands in western North America (Ffolliott and Clary 1982). These studies have reported the response of forage classes, grasses and forbs, to overstory parameters such as canopy cover and basal area. Most have concluded that herbaceous understory vegetation exhibits greater growth when the competing overstory is reduced. Recent work on understory-overstory relationships in the Black Hills has related production of graminoids, forbs, and shrubs to various growing stock levels of *Pinus ponderosa* in both sapling and pole stands (Uresk and Severson 1989).

However, conventions governing management of public lands are changing. Emphasis is being placed on ecosystem management. This approach blends social, physical, economic, and biological needs and values to assure productive, healthy ecosystems (Kaufmann et al. 1994). Key features of ecosystem management are the protection and restoration of biodiversity, which Kaufmann et al. (1994) define as the variety of life and its processes, including variety in genes, species, and ecosystems, and the ecological processes that connect everything in ecosystems. Practical application of principles of ecosystem management will require more specific data. In the case of understory-overstory relationships, this means a better understanding of responses by plant species, rather than groups of species such as grasses, forbs, and shrubs.

The purpose of this paper is to describe how individual plant species responded to changes in basal area of *Pinus ponderosa* and to discuss how these responses could affect plant species richness in the understory of *Pinus ponderosa* forest in the Black Hills. This study was designed to test the null hypothesis that understory production does not differ by species due to changes in *Pinus ponderosa* growing stock levels.

STUDY AREA

The study was conducted on the Black Hills Experimental Forest, about 30 km west of Rapid City, South Dakota. The overstory within the experimental forest is dominated by *Pinus ponderosa*. Understory shrubs[2] include *Arctostaphylos uva-ursi* (bearberry), *Prunus*

[1]Center for Great Plains Ecosystem Research, Rocky Mountain Research Station, School of Mines Campus, Rapid City, SD 57701.
[2]Seedling trees were classified as shrubs for this study.

virginiana (common chokecherry), *Berberis repens* (Oregon grape), *Amelanchier alnifolia* (Saskatoon serviceberry), and *Symphoricarpos* spp. (snowberry). Common herbs include *Oryzopsis asperfolia* (roughleaf ricegrass), *Danthonia intermedia* (timber oatgrass), *Carex* spp. (sedges), *Poa pratensis* (Kentucky bluegrass), *Lathyrus ochroleucus* (cream peavine), and *Campanula rotundifolia* (bluebell). Most of the experimental forest is dominated by the *Pinus ponderosa/Arctostaphylos uva-ursi* habitat type (Hoffman and Alexander 1987) or HU-5, *Pinus ponderosa/Symphoricarpos alba/Arctostaphylos uva-ursi*, as described by Thilenius (1972).

The experimental forest encompasses about 1375 ha and elevations range from 1620 m to 1800 m. Average annual precipitation is 600 mm, 70% of which falls from April through September. Soils are primarily gray wooded, shallow to moderately deep, and derived from metamorphic rock (Boldt et al. 1983).

METHODS

Eight growing stock levels (GSL) of *Pinus ponderosa* including clearcuts and unthinned controls were sampled in both sapling- and pole-sized stands. These GSLs were numerically designated as 0, 5, 9, 14, 18, 23, 28 m^2 ha^{-1}, and unthinned. Growing stock indicates all living trees in a stand. Growing stock level is the basal area (m^2 ha^{-1}) of a stand adjusted to account for differences in the average size of trees left in the stand after thinning. Therefore, the numerical designation of GSL approximates, but does not necessarily equal, the actual basal area of the stand. Basal area of 0 m^2 ha^{-1} indicated clearcut plots. Average basal areas of unthinned pole stands ranged from 37 to 40 m^2 ha^{-1} in 1981, while unthinned sapling stands varied from 27 to 33 m^2 ha^{-1}. Three replicated plots were randomly assigned from a total of 48 plots and installed for each GSL from 5 to unthinned in sapling- and pole-sized stands in 1963. Stem diameters were 8–10 cm in sapling-sized stands, and 15–18 cm in pole-sized stands when treatments were installed. Three replicated clearcut plots in each of the sapling- and pole-sized stands were selected and treated in 1966. Cut material was removed from all plots. Each of the 24 plots in sapling stands was 0.1 ha and the 24 pole stands were each 0.2 ha. All GSLs were sampled in 1976; but budget restrictions resulted in sampling only 5 levels (0, 5, 14, 23 m^2 ha^{-1}, and unthinned) in 1974 and 1981.

Production of understory vegetation was measured during August 1974, 1976, and 1981 on six 15-m randomly placed transects per plot. Twelve 30 × 61-cm quadrats were randomly located along each transect in 1974 and 1976. These data indicated that an increase in number of quadrats would provide a better estimate of minor plant species. Therefore, in 1981, 25 circular plots measuring 0.125 m^2 each were systematically located along 5 of the transects. Current annual growth of all herbage was harvested at ground level for each species. All leaves and terminal portions of twigs to the first node were clipped on shrubs, also by species. Material was oven-dried at 60°C for 48 h and weighed. Weights were averaged and expressed as mean per plot for data analysis.

Heterogeneous variances were present, so data were transformed using a $\log_{(n)}+1$ transformation, analyzed with a one-way analysis of variance (years and stands analyzed separately) and means separated by Tukey's-HSD procedure. In those cases where heterogeneous variances persisted, means were separated using Dunnett's T3 (Dunnett 1980). Statistical inferences were made at a probability level of 0.1 for type I error to decrease type II error.

Plant nomenclature follows Great Plains Flora Association (1986) and Van Bruggen (1985).

RESULTS AND DISCUSSION

Several variables for this study were controlled to reduce variability. Effects of tree size class were separated, all plots were replicated 3 times on the same soil type and had similar site indices, all stands were approximately 70 yr old when treatments were applied, and data were collected over 3 separate years. High natural variability in the understory among replications was common despite this control. As a result, statistical tests often revealed nonsignificant differences despite widely separated means. The common occurrence of heterogeneous variances resulted in analysis via Dunnett's T3, a conservative test. Therefore, the standard error is as important as the mean values in the tables, especially values for individual species.

Relationships between overstory and general categories of understory (graminoids, forbs,

TABLE 1. Understory production (kg ha^{-1}, oven-dried basis) for 1974 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron caninum	204 ± 100	73 ± 43	7 ± 4		<1
Bromus marginatus	1 ± 1				
Bromus porteri		2 ± 2			
Carex spp.	239 ± 123[a]	335 ± 232[a]	25 ± 5[b]	5 ± 4[b]	4 ± 2[b]
Danthonia intermedia	19 ± 7	47 ± 20	47 ± 2	11 ± 5	2 ± 1
Elymus spp.				2 ± 2	
Festuca octoflora			<1		
Koeleria pyramidata	8 ± 4				
Oryzopsis asperifolia	144 ± 41[ab]	304 ± 44[a]	124 ± 88[ab]	62 ± 48[b]	30 ±5[b]
Oryzopsis pungens			3 ± 3		
Poa pratensis	60 ± 42	42 ± 23			
Poa interior		3 ± 3	5 ± 5		<1
Schizachne purpurascens			1 ± 1		
Total	676 ± 110[a]	806 ± 231[a]	212 ± 91[ab]	81 ± 41[b]	36 ± 4[b]
FORBS					
Achillea millefolium	57 ± 21	30 ± 14	2 ± 1	1 ± 1	<1
Agoseris glauca	1 ± 1				
Anaphalis margaritacea				2 ± 2	
Antennaria neglecta		3 ± 2	1 ± 1	1 ± 1	<1
Apocynum androsaemifolium		<1		<1	<1
Artemisia spp.	<1				
Aster spp.	<1				
Aster laevis	<1		<1	1 ± 1	
Astragalus adsurgens	5 ± 5				
Astragalus alpinus		8 ± 4	12 ± 6	1 ± 1	2 ± 2
Astragalus tenellus			1 ± 1		
Campanula rotundifolia	5 ± 3	11 ± 4	<1	<1	

shrubs, and total) aboveground biomass production were previously reported (Uresk and Severson 1989).

Graminoid Response

Carex spp., *Oryzopsis asperfolia,* and *Agropyron caninum* were the most productive species under sapling stands (Tables 1–3). Only *Carex* spp. and *Oryzopsis asperfolia* produced significantly more herbage at GSL 14 m^2 ha^{-1} and below. *Poa pratensis* and *Danthonia intermedia* were also common under saplings but biomass of both was lower. Only *Oryzopsis asperfolia* and *Danthonia intermedia* were common in GSLs above 18 m^2 ha^{-1}. Trends noted in pole-sized stands were somewhat similar (Tables 4–6). One of the most important differences between sapling and pole stands, however, was that *Carex* spp. and *Oryzopsis asperfolia* produced relatively less in pole stands than in sapling stands, whereas *Danthonia intermedia* produced more, particularly in clearcuts. As in sapling stands, significant differences by species among GSLs were rare. Only *Carex* spp. were found to produce more at lower GSLs in 1981 (Table 6).

The general responses of graminoids in both sapling and pole stands were similar to other Black Hills studies that included data on species (Pase 1958, Wrage 1994). Pase (1958) limited descriptions to the most important species (the rest were combined into an "other" category); but Wrage's descriptions (1994) were complete. Pase's study included a variety of sites throughout the Black Hills; and Wrage's study area, on soils similar to ours but a different habitat type, was about 10.5 km SE and 350 m lower in elevation than the experimental forest where this study was conducted.

Both studies reported responses similar to those herein, but some important differences were evident. Pase (1958) found that significant

TABLE 1. Continued.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	14	23	Unthinned
Cirsium spp.	36 ± 36				
Delphinium bicolor	<1				
Erigeron spp.	3 ± 3	<1			<1
Fragaria vesca	9 ± 5	9 ± 7	4 ± 3	2 ± <1	<1
Galium boreale	3 ± 3				<1
Lactuca spp.		<1	1 ± 1		
Lathyrus ochroleucus	5 ± <1^{a}	27 ± 5^{b}	12 ± 7^{ab}	7 ± 4^{ab}	1 ± <1^{a}
Linnaea borealis				17 ± 17	<1
Oxytropis sericea				<1	
Solidago spp.			<1		
Taraxacum officinale	<1	<1	<1		
Vicia americana	<1	<1	<1		<1
Viola spp.	8 ± <1	12 ± 10	1 ± <1	1 ± <1	1 ± <1
Zizia aptera	<1				
Total	134 ± 39^{a}	102 ± 16^{ab}	37 ± 14^{ab}	34 ± 22^{ab}	8 ± 4^{b}
SHRUBS					
Amelanchier alnifolia	3 ± 2			1 ± <1	
Arctostaphylos uva-ursi	244 ± 74	205 ± 56	293 ± 78	255 ± 48	50 ± 7
Berberis repens				8 ± 8	
Populus tremuloides	1 ± 1	<1	<1	<1	<1
Rosa woodsii	7 ± 3	7 ± 5	4 ± 3	4 ± <1	1 ± <1
Rubus idaeus	28 ± 23	23 ± 7	5 ± 4		
Shepherdia canadensis				9 ± 9	
Spiraea betulifolia	2 ± 2	1 ± <1	1 ± <1	4 ± 2	1 ± <1
Symphoricarpos spp.	18 ± 8	7 ± 2	4 ± 3	3 ± 1	1 ± <1
Vaccinium scoparium				21 ± 21	
Total	303 ± 108^{a}	244 ± 57^{a}	308 ± 76^{a}	305 ± 20^{a}	54 ± 6^{b}
GRAND TOTAL	1113 ± 115^{a}	1152 ± 196^{a}	557 ± 138^{ab}	420 ± 57^{b}	98 ± 11^{c}

amounts of *Oryzopsis asperfolia* persisted under moderately dense canopy cover (40–59%, 19–27 m^2 ha^{-1} basal area) and dense canopy cover (60–71%, 28–33 m^2 ha^{-1} basal area), which compared with our findings. Pase (1958) and Wrage (1994) used canopy cover in their papers; we converted these to basal area estimates using Bennett's (1984) model: % canopy cover = $0.51BA(ft^2\ ac^{-1}) - 1.94$, $R^2 = 0.83$. Wrage (1994) did not find *Oryzopsis asperfolia* in his plots. Both Pase and Wrage noted that *Danthonia* (oatgrass) was most abundant under intermediate pine canopies. We found the same relationship under sapling stands, but in pole stands *Danthonia* was more abundant in clearcuts than in other GSLs. *Poa*, the most abundant grass component in open stands studied by both Pase and Wrage, was common but subdominant in this study. Pase (1958) listed *Poa pratensis*, *Sporobolus heterolepis* (prairie dropseed), and *Carex* spp. as the most common graminoids in pine cover class 0–19% (0–9 m^2 ha^{-1} basal area). Wrage (1994) listed *Poa*, *Carex* spp., and the exotic *Bromus inermis* (smooth brome) as being most common in open stands (<30% pine cover, 14 m^2 ha^{-1} basal area). We found *Agropyron caninum*, *Carex* spp., and *Oryzopsis asperfolia* most abundant in 0 and 5 GSL sapling stands and *Danthonia*, *Carex* spp., and *Agropyron caninum* most abundant in pole stands.

We considered 11 species as uncommon in sapling stands, defining uncommon as producing <5 kg ha^{-1} in ≤3 stands over all years (Tables 1–3). Included among these were *Bromus marginata* (mountain brome), *Schizachne purpurascens* (false melic), *Oryzopsis pungens* (mountain ricegrass), and the exotic *Agropyron cristatum* (crested wheatgrass). There were 10 uncommon graminoid species in the understory of pole-sized stands (Tables 4–6). Two of these, *Bromus marginatus* and *Oryzopsis*

TABLE 2. Understory production (kg ha^{-1}, oven-dried basis) for 1976 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	9	14	18	23	28	Unthinned
GRAMINOIDS								
Agrostis stolonifera	<1	2 ± 2	2 ± <1	1 ± 1		<1	<1	<1
Agropyron caninum	144 ± 81	101 ± 64	100 ± 22	26 ± 20	18 ± 9			<1
Carex spp.	595 ± 290	261 ± 228	55 ± 37	49 ± 10	28 ± 17	8 ± 4	10 ± 7	14 ± 7
Danthonia intermedia	36 ± 20	67 ± 22	87 ± 36	77 ± 13	55 ± 28	41 ± 14	3 ± 2	1 ± <1
Koeleria pyramidata					<1			
Oryzopsis asperifolia	71 ± 46	311 ± 160	83 ± 45	298 ± 182	107 ± 43	67 ± 15	26 ± 11	42 ± 19
Oryzopsis pungens	2 ± 1	3 ± 3	2 ± 1	<1	4 ± 4	<1		
Poa pratensis	19 ± 18	50 ± 16	12 ± 9	3 ± 3	3 ± 2			
Stipa comata						10 ± 10		
Unknown grass		<1						
Total	867 ± 247[a]	796 ± 81[a]	340 ± 79[ab]	454 ± 187[ab]	216 ± 74[abc]	127 ± 18[bc]	39 ± 19[c]	57 ± 24[c]
FORBS								
Achillea millefolium	133 ± 39	37 ± 19	30 ± 8	10 ± 7	6 ± 3	8 ± 5	2 ± 2	
Antennaria neglecta	4 ± 4	4 ± 2	4 ± 4	2 ± 2	1 ± 1	6 ± 4		<1
Apocynum androsaemifolium		<1	3 ± 1				<1	<1
Aster laevis	<1			<1				
Astragalus adsurgens	12 ± 6	41 ± 28	29 ± 9	17 ± 14	2 ± 2	6 ± 3	6 ± 2	2 ± 2
Campanula rotundifolia	34 ± 19	12 ± 6	<1		1 ± 1	<1		1 ± <1
Chenopodium capitatum			99 ± 99					
Cirsium spp.				6 ± 6				
Delphinium bicolor	<1		<1					
Erigeron subtrinervis	2 ± 2	11 ± 11	2 ± 2			<1		<1
Fragaria vesca	15 ± 4	5 ± 1	9 ± 3	3 ± 3	8 ± 3	<1	<1	2 ± 2
Galium boreale	31 ± 31		4 ± 2	2 ± 2	2 ± 1	1 ± 1		
Lathyrus ochroleucus	15 ± 4	113 ± 5	83 ± 14	23 ± 9	36 ± 7	20 ± 11	10 ± 5	7 ± 6
Solidago spp.			2 ± 2					

TABLE 2. Continued.

	Clearcuts	Growing stock levels ($m^2\ ha^{-1}$) 5	9	14	18	23	28	Unthinned
FORBS (continued)								
Taraxacum officinale	<1							
Trifolium repens	<1	3 ± 3	5 ± 5					
Unknown forb	20 ± 15	6 ± 5	5 ± 5	<1				
Vicia americana	17 ± 9	11 ± 2	22 ± 8	2 ± 2	2 ± 1			
Viola adunca	13 ± 2	5 ± 1	4 ± 4	3 ± 3	<1	<1	<1	1 ± 1
Total	296 ± 33^{a}	246 ± 38^{ab}	306 ± 86^{a}	64 ± 16^{abc}	59 ± 16^{abc}	43 ± 11^{bc}	19 ± 8^{c}	15 ± 9^{c}
SHRUBS								
Amelanchier alnifolia	<1	<1	9 ± 6	5 ± 3	6 ± 3	4 ± 3	<1	<1
Arctostaphylos uva-ursi	760 ± 354	1095 ± 411	1081 ± 255	753 ± 326	1243 ± 185	553 ± 344	787 ± 327	260 ± 114
Berberis repens			3 ± 3			10 ± 10		1 ± 1
Populus tremuloides	98 ± 81		<1	<1				
Prunus virginiana					1 ± 1		<1	
Rosa woodsii	9 ± 3^{ab}	18 ± 12^{a}	10 ± 3^{ab}	9 ± 5^{ab}	$7 \pm <1^{b}$	6 ± 2^{b}	$1 \pm <1^{b}$	$2 \pm <1^{b}$
Rubus idaeus	70 ± 70^{a}	29 ± 12^{ab}	45 ± 6^{a}	4 ± 4^{b}	6 ± 4^{b}			$<1^{b}$
Shepherdia canadensis			85 ± 85			7 ± 7		
Symphoricarpos spp.	24 ± 15	14 ± 12	23 ± 1	7 ± 5	5 ± 3	3 ± 1	2 ± 1	$1 \pm <1$
Unknown shrub	2 ± 2							
Vaccinium scoparium						14 ± 14		4 ± 4
Total	964 ± 411	1156 ± 54	1255 ± 233	778 ± 331	1267 ± 178	597 ± 330	791 ± 329	269 ± 111
GRAND TOTAL	2126 ± 196^{ab}	2199 ± 70^{a}	1901 ± 280^{ab}	1296 ± 128^{abc}	1542 ± 113^{abc}	1202 ± 327^{abc}	850 ± 342^{bc}	341 ± 138^{c}

TABLE 3. Understory production (kg ha^{-1}, oven-dried basis) for 1981 in sapling-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron cristatum			1 ± 1		
Agropyron spicatum		9 ± 9			
Agropyron caninum	282 ± 48	74 ± 19	24 ± 24	6 ± 4	
Bromus marginatus			<1		
Carex spp.	508 ± 232^{a}	429 ± 160^{a}	105 ± 56^{ab}	26 ± 13^{b}	15 ± 13^{b}
Danthonia intermedia	48 ± 8	141 ± 27	49 ± 16	15 ± 11	4 ± 3
Festuca ovina		<1	1 ± >1		
Koeleria pyramidata	1 ± >1	3 ± 3			
Oryzopsis asperifolia	176 ± 8^{ab}	393 ± 49^{a}	237 ± 121^{a}	70 ± 17^{b}	59 ± 24^{b}
Oryzopsis pungens	2 ± 2			1 ± 1	
Poa pratensis	252 ± 67	1 ± 1			
Poa interior	27 ± 18	16 ± 7		<1	
Unknown grass	1 ± 1	23 ± 0	2 ± 2		<1
Total	1297 ± 263^{a}	1089 ± 142^{a}	424 ± 177^{ab}	118 ± 15^{b}	79 ± 35^{b}
FORBS					
Achillea millefolium	88 ± 42	52 ± 17	9 ± 4	3 ± 3	2 ± 1
Agoseris glauca	14 ± 6				
Antennaria neglecta	2 ± 2	5 ± 3	1 ± 1	2 ± 1	1 ± <1
Apocynum androsaemifolium	<1	3 ± 2	2 ± 1	5 ± 4	1 ± 1
Astragalus canadensis			3 ± 2		
Astragalus adsurgens	20 ± 4	17 ± 6	4 ± 3	3 ± 3	2 ± 2
Astragalus spp.		1 ± 1		<1	
Astragalus tenellus	12 ± 6	6 ± 3	5 ± 5	5 ± 5	5 ± 5
Campanula rotundifolia	25 ± 5	8 ± 2	1 ± 1		<1
Cirsium vulgare	17 ± 13	1 ± 1		<1	
Delphinium bicolor					<1
Erigeron spp.	5 ± 5	1 ± <1	<1	<1	
Fragaria vesca	33 ± 2^{a}	24 ± 15^{ab}	7 ± 5^{b}	3 ± <1^{b}	2 ± 1^{b}

pungens, also occurred in sapling stands. Others included *Koelaria cristata* (prairie junegrass), which was common in sapling stands, *Poa arida* (plains bluegrass), *Bromus porteri* (nodding brome), and the exotic *Phleum pratense* (timothy). All uncommon species occurred in pine stands stocked at ≤14 m^2 ha^{-1} basal area. Wrage (1994: Appendix D) had 8 grass species that contributed <1% foliar cover in ≤3 stands over all years and all *Pinus ponderosa* cover classes: *Agropyron repens* (quackgrass), *A. intermedium* (intermediate wheatgrass), *Bouteloua curtipendula* (sideoats grama), *Calamagrostis rubescens* (pine reedgrass), *Muhlenbergia torreyi* (ring muhly), *Schizachne purpurascens, Sporobolus asper* (rough dropseed), and *Stipa spartea* (porcupine grass).

Three exotic grasses were found under the pine overstory; one, *Agrostis stolonifera* (redtop), was common but scattered. The others, *Agropyron cristatum* and *Phleum pratense,* occurred only in a single stand each. *Poa pratensis* was not considered exotic because it occurs in both naturalized and native forms in this area (Great Plains Flora Association 1986). Wrage (1994) reported 3 exotic grasses: *Agropyron repens, Agropyron intermedium,* and *Bromus inermis.*

Altogether, we found and identified 22 different graminoids in the pine understory in this study. Thirteen were common to sapling- and pole-sized stands while 3 and 2 species were unique to each respective size class. Pase (1958) reported 38 graminoid species and Wrage (1994) listed 23.

An average of 9 graminoid species occurred in GSLs 0, 5, and 14 m^2 ha^{-1} over all years. This was higher ($P < 0.05$) than the 6 and 5 species found in GSL 23 and unthinned stands, respectively (Uresk and Severson 1989). The mean number of species present in pole clearcuts (11) and GSL 5 m^2 ha^{-1} (10) was

TABLE 3. Continued.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	14	23	Unthinned
Galium boreale	18 ± 13	1 ± 1	2 ± 2		<1
Hieracium canadense		<1		1 ± 1	
Iris missouriensis		<1			
Lathyrus ochroleucus	40 ± 20	117 ± 28	68 ± 33	39 ± 13	10 ± 6
Linnaea borealis			<1	2 ± 2	<1
Lupinus spp.	3 ± 3			7 ± 4	
Monarda fistulosa	1 ± 1			1 ± 1	
Polygonum persicaria	1 ± 1				
Smilacina stellata			2 ± 2		
Solidago sparsiflora	7 ± 4	6 ± 5	<1	11 ± 11	<1
Taraxacum officinale	1 ± 1	<1			
Trifolium repens	1 ± 1	4 ± 4		11 ± 11	<1
Vicia americana	57 ± 35[a]	12 ± 2[b]	9 ± 9[b]	2 ± 2[b]	1 ± 1[b]
Viola adunca	25 ± 1	18 ± 3	2 ± 2	1 ± 1	1 ± 1
Total	369 ± 99[a]	276 ± 6[a]	117 ± 52[abc]	92 ± 10[bc]	26 ± 16[c]
SHRUBS					
Amelanchier alnifolia	2 ± 1		1 ± 1	1 ± 1	<1
Arctostaphylos uva-ursi	604 ± 179	820 ± 95	872 ± 427	821 ± 333	205 ± 111
Berberis repens				8 ± 8	4 ± 4
Populus tremuloides	1 ± 1		3 ± 3		
Rosa woodsii	25 ± 2	21 ± 12	13 ± 8	11 ± 6	3 ± 3
Rubus idaeus	130 ± 117	61 ± 24	22 ± 13	1 ± 1	3 ± 3
Shepherdia canadensis				9 ± 9	7 ± 7
Spiraea betulifolia	1 ± 1	1 ± <1	7 ± 2	8 ± 4	4 ± 2
Symphoricarpos spp.	38 ± 10	12 ± 4	20 ± 13	5 ± 3	3 ± 2
Vaccinium scoparium				1 ± 1	
Total	802 ± 307	915 ± 126	938 ± 428	866 ± 326	230 ± 107
GRAND TOTAL	2450 ± 168[a]	2280 ± 102[a]	1478 ± 596[ab]	1076± 330[ab]	334 ± 146[b]

greater ($P < 0.05$) than the 5, 5, and 3 species found in GSLs 14, 23, and unthinned stands, respectively (Uresk and Severson 1989). Wrage (1994) counted 20, 19, and 16 grass species in his open (tree cover <30%, 14 m^2 ha^{-1} basal area), intermediate (30–60%, 14–27 m^2 ha^{-1}), and dense (>60%, 27 m^2 ha^{-1}) *Pinus ponderosa* stands, respectively.

Forb Response

Forb response, relative to GSLs, was similar to that of graminoids except that forbs produced about 30% less forage (Tables 1–6). No single forb species dominated any GSL of either size class; however, *Achillea millifolium* (common yarrow), *Campanula rotundifolia,* and *Lathyrus ochroleucus* were the most common forbs found in pole stands (Tables 4–6). *Achillea millifolium* and *Lathyrus ochroleucus* were the most abundant forbs in sapling stands (Tables 1–3), but few significant differences by species among GSLs were noted. *Lathyrus ochroleucus* produced more herbage in mid-level GSL sapling stands (5–23) in 1974 (Table 1), and *Fragaria vesca* (woodland strawberry) and *Vicia americana* (American vetch) produced more in clearcuts in 1981 (Table 3), but no differences were noted in pole stands. Pase (1958) reported *Trifolium repens* (white clover), *Fragaria vesca*, and *Achillea millifolium* to be abundant in open stands, but only *Lathyrus ochroleucus* and *Solidago* spp. (goldenrod) persisted under moderately dense pine canopies. *Artemisia ludoviciana* (white sagewort), *Glycyrrhiza lepidota* (wild licorice), *Psoralea argophylla* (silverleaf scurfpea), and *Monarda fistulosa* (wild bergamot) were the most common forbs in Wrage's (1994) open stands, but only *Glycyrrhiza lepidota* persisted into intermediate stands. Forbs were scarce in his dense

TABLE 4. Understory production (kg ha^{-1}, oven-dried basis) for 1974 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	14	23	Unthinned
GRAMINOIDS					
Agrostis stolonifera	<1				
Agropyron spicatum	3 ± 2	<1			
Agropyron caninim	155 ± 89	3 ± 2	<1		
Bromus marginatus		<1			
Bromus porteri		2 ± 2	<1		
Carex spp.	7 ± 4	15 ± 9	2 ± <1	10 ± 5	<1
Danthonia intermedia	322 ± 21	135 ±31	46 ± 17	5 ± 2	
Festuca octoflora	20 ± 10	<1			
Festuca ovina	<1	2 ± 1			
Koeleria pyramidata	3 ± 3				
Oryzopsis asperifolia	9 ± 8	29 ± 24		17 ± 15	4 ± 3
Poa spp.	10 ± 4				
Poa pratensis	7 ± 4	4 ± 4			
Total	538 ± 76^{a}	193 ± 45^{ab}	48 ± 15^{b}	32 ± 17^{bc}	5 ± 4^{c}
FORBS					
Achillea millefolium	39 ± 11	6 ± 3	1 ± 1	1 ± 1	<1
Antennaria neglecta	7 ± 4	9 ± 9	9 ± 6	3 ± 2	
Apocynum androsaemifolium	<1	1 ± <1	<1	<1	<1
Astragalus alpinus	13 ± 3	17 ± 11	<1	1 ± 1	
Astragalus tenellus	4 ± 3	3 ± 3		3 ± 3	
Astragalus spp.	3 ± 3	<1	1 ± 1	<1	
Campanula rotundifolia	35 ± 22	6 ± 2		<1	
Cirsium arvense	14 ± 14				
Cirsium vulgare	15 ± 8				
Erigeron spp.	2 ± 1	4 ± 1	1 ± 1	<1	
Fragaria vesca	3 ± 2	<1	<1	<1	

stands; those most common were *Galium boreale* (northern bedstraw) and *Smilacina stellata* (false Solomon's seal).

Many forb species occurred under the pine canopy, but they contributed little to total aboveground biomass. We categorized 22 species as uncommon, using "uncommon" as we defined it for graminoids. Wrage (1994) also noted many forbs that were generally scarce. If we arbitrarily classify uncommon species in Wrage's study as those having <1% foliar cover in ≤3 pine cover classes over all years, 18 forb species would be considered uncommon (Wrage 1994: Appendix D).

Nine of the forbs found in the pine understory are exotic species. Only 2, however, were common: *Taraxacum officinale* (common dandelion) and *Trifolium repens*. These species are both ubiquitous over North America. Two others, both noxious weeds, *Cirsium arvense* (Canada thistle) and *C. vulgare* (bull thistle), were common only locally. Another, *Linaria vulgaris* (butter-and-eggs), was found only in pole clearcuts. The other 4, *Polygonum persicaria* (lady's thumb), *Tragopogon dubius* (goats beard), *Sisymbrium altissimum* (tumbling mustard), and *Rumex acetosella* (sheep sorrel), were rare. A large amount of *Chenopodium capitatum* (strawberry blite) was found in 1 plot of 1 replicate of sapling GSL 9 m^2 ha^{-1} in 1976 (Table 2). It is unknown whether this species is indigenous or exotic (Great Plains Flora Association 1986). Wrage (1994) listed 4 exotic species, *Cirsium arvense, Convolvulus arvense* (field bindweed), *Taraxacum officinale*, and *Tragopogon dubius*. All were classed as uncommon except *Convolvulus arvense*, which was common in open stands.

Although our aboveground biomass estimates of forbs were less than for graminoids, there were more forb species than graminoid species. Fifty-three forbs, including 15 identified only to genus, grew in the understory; 25 identified species were common to both

TABLE 4. Continued.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	14	23	Unthinned
Galium boreale		<1		<1	
Iris missouriensis	1 ± 1		<1		
Lactuca spp.		5 ± 2	3 ± 1	8 ± 7	<1
Lathyrus ochroleucus	7 ± 6				
Linaria vulgaris	<1				
Oxytropis sericea		6 ± 4	9 ± 7	<1	
Potentilla spp.	<1				
Solidago spp.	3 ± 3	<1		1 ± 1	
Taraxacum officinale	<1	<1			
Trifolium repens	5 ± 5	23 ± 23		<1	
Vicia americana	2 ± 2	<1	<1	<1	
Viola spp.	5 ± <1	3 ± 2			
Total	161 ± 15[a]	86 ± 35[ab]	28 ± 5[b]	22 ± 7[b]	<1[c]
SHRUBS					
Amelanchier alnifolia	1 ± 1	5 ± 5	<1		
Arctostaphylos uva-ursi	209 ± 7	305 ± 94	306 ± 72	135 ± 35	66 ± 58
Berberis repens		19 ± 19			
Betula papyrifera	<1				
Juniperus communis	<1				
Populus tremuloides	21 ± 21	<1			
Rosa woodsii	10 ± 8	<1	2 ± 2	<1	<1
Rubus idaeus	49 ± 17	10 ± 6			
Shepherdia canadensis				10 ± 10	
Spiraea betulifolia	1 ± <1	3 ± 2	<1	1 ± <1	
Symphoricarpos spp.	7 ± 7	3 ± 3	2 ± 2	2 ± 2	<1
Total	299 ± 48	347 ± 77	311 ± 70	149 ± 43	67 ± 58
GRAND TOTAL	998 ± 84[a]	626 ± 46[b]	387 ± 87[bc]	203 ± 34[bc]	72 ± 58[c]

saplings and poles, while 6 and 7 species were unique to the sapling and pole understories, respectively. Pase (1958) and Wrage (1994) noted 63 and 41 forb species in their respective studies.

We found an average of 18 forb species over all years in clearcut sapling stands, which was significantly higher ($P < 0.05$) than the 15, 13, and 13 species found in GSLs 5, 14, and 23 m^2 ha^{-1}, respectively. Eleven species were found in unthinned stands, fewer ($P < 0.05$) than in clearcuts (Uresk and Severson 1989). Trends were similar in pole-sized stands. Twenty-one species were found in clearcuts and 18 in GSL 5, which was higher ($P < 0.05$) than the 12 and 13 found in GSLs 14 and 23. Fewest species (5) were found in unthinned pole stands (Uresk and Severson 1989). Wrage (1994) counted 36, 29, and 24 forbs in *Pinus* stands with open, intermediate, and dense canopy covers.

Shrub Response

Mean shrub production was similar across all *Pinus ponderosa* sapling stocking levels in 1976 and 1981 and in 1974 pole stands. In the remaining sapling (1974) and pole (1976, 1981) stands, all growing stock levels produced more shrubs than unthinned stands. In general, shrub production tended to be somewhat higher at mid-levels than in clearcuts and much higher than in unthinned stands, although differences among lower GSLs were not significant (Tables 1–6). *Arctostaphylos uva-ursi* accounted for most shrub production in all stands regardless of size class or stocking levels, but differences were not significant except in pole stands in 1981 (Table 6). Production of *Arctostaphylos uva-ursi* was 75–99% of total shrub production in sapling stands and 70–99% in pole stands. Lower percentages tended to occur in clearcuts. Higher proportions of *Rubus idaeus* (red raspberry) and *Symphoricarpos* spp. (snowberry) were found in clearcuts. *Rosa woodsii* and

TABLE 5. Understory production (kg ha^{-1}, oven-dried basis) for 1976 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})						
	Clearcuts	5	9	14	18	23	28	Unthinned
GRAMINOIDS								
Agrostis stolonifera	3 ± 2	1 ±<1	<1	1 ± <1			<1	
Agropyron caninum	71 ± 11	52 ± 22	14 ± 8	2 ± 2	6 ± 6		1 ± 1	<1
Carex spp.	52 ± 20	32 ± 21	8 ± 7	5 ± 3	25 ± 23	6 ± 3	<1	1 ± <1
Danthonia intermedia	406 ± 69	180 ± 58	116 ± 27	196 ± 17	70 ± 28	37 ± 19	32 ± 12	4 ± 3
Festuca ovina	10 ± 5	2 ± 1						
Oryzopsis asperifolia	70 ± 70	38 ± 38	12 ± 12		2 ± 2	5 ± 5		4 ± 2
Oryzopsis pungens	<1	5 ± 3	<1		8 ± 7	<1	<1	
Poa pratensis	23 ± 21	27 ± 25	<1		3 ± 3			
Stipa spp.			3 ± 3					
Unknown grass		3 ± 3	6 ± 6					
Total	633 ± 30^{a}	341 ±120^{ab}	162 ± 22^{b}	205 ± 18^{b}	114 ± 46^{bc}	48 ± 26^{c}	35 ± 14^{c}	10 ± 5^{c}
FORBS								
Achillea millefolium	121 ± 19	27 ± 23	<1	4 ± 4	1 ± <1	<1	1 ± 1	
Agoseris glauca					<1			
Antennaria neglecta	25 ± 10	15 ± 15	4 ± 1	7 ± 4	1 ± <1	5 ± 5	1 ± <1	<1
Apocynum androsaemifolium	5 ± 3	7 ± 6			<1			
Aster laevis	3 ± 3	4 ± 4	2 ± 2	5 ± 4	<1	<1	<1	
Astragalus adsurgens	37 ± 12	24 ± 12	20 ± 13	24 ± 12	6 ± 4	5 ± 4	8 ± 5	<1
Campanula rotundifolia	88 ± 34	8 ± 4	1 ± 1	1 ± 1	4 ± 3	<1		
Cirsium vulgare	20 ± 10	10 ± 10						
Delphinium bicolor	<1	<1						
Erigeron subtrinervis	10 ± 5		<1		<1		<1	
Frageria vesca	3 ± 2	1 ± 1	3 ± 2	1 ± 1	1 ± 1	<1	<1	
Galium boreale		<1			<1	<1		
Lathyrus ochroleucus	25 ± 8	36 ± 10	30 ± 13	18 ± 11	35 ± 12	10 ± 5	10 ± 2	2 ± 1
Linaria vulgaris	26 ± 24	<1						

TABLE 5. Continued.

	Clearcuts	Growing stock levels (m^2 ha^{-1}) 5	9	14	18	23	28	Unthinned
FORBS (continued)								
Sisymbrium altissimum		1 ± 1						
Solidago spp.			1 ± 1					
Solidago missouriensis	6 ± 6							
Taraxacum officinale	2 ± <1	<1						
Tragopogon dubius	<1							
Trifolium repens	46 ± 9	6 ± 6		9 ± 6				
Unknown forb	41 ± 21	3 ± 1	7 ± 7	<1	<1			
Vicia americana	2 ± 2	8 ± 8	<1 ± <1	2 ± 1	5 ± 3	4 ± 4	1 ± 1	
Viola adunca	16 ± 11	13 ± 7	2 ± 2	<1 ± <1	<1		<1	
Total	477 ± 82[a]	164 ± 36[ab]	74 ± 33[b]	73 ± 31[b]	56 ± 23[b]	27 ± 8[b]	24 ± 5[b]	3 ± 1[c]
SHRUBS								
Amelanchier alnifolia	8 ± 3	11 ± 6	6 ± 3	4 ± 4	6 ± 4	2 ± 1	1 ± <1	1 ± <1
Arctostaphylos uva-ursi	687 ± 187	827 ± 428	1124 ± 279	934 ± 277	507 ± 186	675 ± 155	422 ± 145	96 ± 94
Berberis repens		65 ± 65			1 ± 1			
Potentilla fruticosa						<1		
Populus tremuloides	9 ± 9	1 ± 1				<1		
Rosa woodsii	21 ± 13	3 ± 3	6 ± 5	3 ± 2	4 ± 3	2 ± 1	<1	<1
Rubus idaeus	82 ± 11	84 ± 55	<1					
Shepherdia canadensis	<1	23 ± 23	81 ± 52		26 ± 26			
Symphoricarpos spp.	14 ± 14	5 ± 2	3 ± 2	7 ± 6	5 ± 2	1 ± 1	2 ± 1	2 ± 1
Total	821 ± 220[ab]	1019 ± 291[a]	1220 ± 265[a]	948 ± 279[ab]	550 ± 161[ab]	681 ± 155[ab]	426 ± 143[ab]	100 ± 94[b]
GRAND TOTAL	1931 ± 132[a]	1523 ± 252[ab]	1456 ± 306[ab]	1226 ± 306[ab]	720 ± 129[bc]	756 ± 127[bc]	485 ± 133[b]	113 ± 96[c]

TABLE 6. Understory production (kg ha^{-1}, oven-dried basis) for 1981 in pole-sized ponderosa pine stands growing at different tree stocking levels, Black Hills, South Dakota. Numbers are means ± standard errors. Values within a row followed by different letters are significantly different at the 0.10 probability level.

		Growing stock levels (m^2 ha^{-1})			
	Clearcuts	5	14	23	Unthinned
GRAMINOIDS					
Agropyron caninum	41 ± 9	26 ± 3	<1	<1	
Aristida purpurea				<1	
Bromus porteri		2 ± 2			
Carex spp.	83 ± 26^{a}	60 ± 23^{a}	7 ± 5^{bc}	14 ± 4^{b}	<1 ± <1^{c}
Danthonia intermedia	651 ± 95	365 ± 60	95 ± 17	30 ± 15	<1
Festuca ovina	17 ± 8	<1	3 ± 3		
Koeleria pyramidata	10 ± 10	4 ± 2	<1		
Oryzopsis asperifolia	11 ± 8	24 ± 13	7 ± 3	15 ± 15	
Oryzopsis pungens	5 ± 5			2 ± 2	
Phleum pratense	1 ± 1				
Poa pratensis	89 ± 37	<1			
Poa interior	5 ± 1	1 ± <1	<1		
Unknown grass	2 ± 2	<1	<1	<1	
Total	916 ± 81^{a}	484 ± 63^{b}	113 ± 26^{c}	61 ± 30^{cd}	4 ± 3^{d}
FORBS					
Achillea millefolium	72 ± 18	15 ± 3	5 ± 3	<1	<1
Agoseris glauca	5 ± 4	<1			
Antennaria neglecta	23 ± 15	7 ± 7	3 ± 3	3 ± 1	1 ± <1
Apocynum androsaemifolium	1 ± <1	5 ± 4	2 ± 2	<1	<1
Astragalus spp.	17 ± 9	2 ± 1	1 ± 1	<1	
Astragalus adsurgens	4 ± 2	21 ± 10	25 ± 13	5 ± 4	
Astragalus canadensis	17 ± 14	34 ± 28	9 ± 9	<1	
Astragalus tenellus	5 ± 3	7 ± 6	5 ± 5	13 ± 6	
Campanula rotundifolia	39 ± 8	5 ± 2	2 ± 2		<1
Cirsium vulgare	1 ± 1				
Delphinium bicolor		<1			
Erigeron subrinervis	10 ± 9	<1	<1	<1	
Fragaria vesca	12 ± 7	7 ± 2	1 ± <1	<1	<1

Rubus idaeus produced more at the 3 lower sapling GSLs in 1976 (Table 2), while *Arctostaphylos uva-ursi* was more abundant in pole clearcuts in 1981 (Table 6). Pase (1958) noted the same patterns of *Arctostaphylos uva-ursi* abundance, but this species did not occur in Wrage's (1994) study area. *Symphoricarpos occidentalis* was the most common shrub noted by Wrage (1994) under all *Pinus* canopy levels. *Juniperus communis* (common juniper), rare on our study site and on Wrage's (1994), was abundant on sites studied by Pase (1958). This species is a predominant constituent of *Pinus ponderosa* understory on limestone-derived soils (Thilenius 1972, Hoffman and Alexander 1987).

Fourteen shrub species occurred under the *Pinus* canopy, 11 of which were common to both sapling and pole-sized stands. One species, *Vaccinium scoparium* (grouseberry), was unique to sapling stands and was common in higher GSLs (Tables 1–3). None of the shrub species under saplings were categorized as uncommon. Three species, all unique to pole-sized stands, were classed as uncommon: *Juniperus communis*, *Betula paperifera* (paper birch), and *Potentilla fruticosa* (shrubby cinquefoil). Pase (1958) counted 18 shrub species, while Wrage (1994) noted only 6.

There were no differences ($P < 0.05$) in number of shrub species among sapling GSLs; they ranged from 6 to 8 across all levels with no apparent pattern. In pole stands 8 shrub species occurred in clearcuts but only 4 species were found in GSL 5 (Uresk and Severson 1989). Wrage (1994) did not note any differences. He found 4 shrub species under open, 5 under intermediate, and 5 under dense *Pinus* canopies. None of the shrubs found in the understory of our study or Wrage's were exotic.