AN ABSTRACT OF THE THESIS OF

Dong Yeob Kim for the degree of Master of Science
in Forest Science presented on May 4, 1987.
Title: Seasonal Estimates of Nitrogen Fixation by *Alnus rubra* and *Ceanothus* Species in Western Oregon Forest Ecosystems

Abstract approved: Kermit Cromack, Jr.
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Two case studies of 5 ecosystems were used to examine the nitrogen fixation rate of red alder (*Alnus rubra* Bong.), varnishleaf (*Ceanothus velutinus* var. *laevigatus* (Hook.) T. & G.), deerbrush (*C. integerrimus* H. & A.), and snowbrush (*C. velutinus* var. *velutinus* Dougl. Ex Hook). The first case study assayed nitrogen fixation of 2-year-old red alder at the Alsea Ranger District of the Siuslaw National Forest and at the OSU Field Laboratory, and 58-year-old red alder at the Cascade Head Experimental Forest. Annual nitrogen fixation was 22.8, 17.5, and 50.1 kg/ha/yr for the Alsea site, OSU Field Laboratory, and Cascade Head, respectively. Red alder showed the potential of substantial nitrogen input into the ecosystem at 2 years and 58 years of age.

The second case study assayed nitrogen fixation of three *Ceanothus* species growing in southwestern Oregon. At

the Waters Creek site, 5- to 6-year-old varnishleaf and deerbrush showed similar nitrogen fixing activity. The seasonal pattern of 11-year-old snowbrush at the Windy Creek site was different from that of the other *Ceanothus* species at the Waters Creek site. Annual nitrogen fixation was 8.3, 0.3, and 69.4 kg/ha/yr for varnishleaf, deerbrush and snowbrush, respectively. Eleven-year-old snowbrush at the Windy Creek site supplied a substantial amount of nitrogen to the ecosystem. Following the attack of California tortoise-shell butterfly, and the subsequent defoliation of snowbrush, annual nitrogen fixation by snowbrush at the Windy Creek site decreased to 34.8 kg/ha/yr. This value was about one half the value for unattacked shrubs.

Red alder can be developed as a tool for forest management at an early stage as well as later stages of growth. *Ceanothus* species can also be used for forest management, especially in dry areas.

Seasonal Estimates of Nitrogen Fixation by Alnus rubra and Ceanothus Species in Western Oregon Forest Ecosystems

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed May 4, 1987

Commencement June 1987

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Date thesis is presented May 4, 1987

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ACKNOWLEDGEMENTS

There are many people who deserve thanks both for helping with this work and for helping to make the three years I have spent here among the most enjoyable of my life.

First of all, I would like to thank my major professor Dr. Kermit Cromack, Jr. who provided the direction, facilities, money, and especially encouragement for my study. His excellent personality has been so much help to a foreign student like me. I also appreciate the comments from the other committee members, Drs. David E. Hibbs, David D. Myrold, and Russell E. Ingham.

I thank Dr. Hibbs and Lauri Shainsky who allowed me to use their 2-year-old seedlings growing at the Alsea site and OSU Field Laboratory, respectively.

I would like to acknowledge the help and general support I have received from the Forest Science faculty, staff, and students, especially Barbara J. Yoder, Carol Glassman, Greg, Jeff, Cindy, Niu, and Koo. I appreciate the help and information that you all provided. THANKS !!

I thank my mother and my wife who have been the greatest in help and encouragement. I must, of course, also thank other family members here and in my country who encouraged me and showed interest in my goals.

Parts of this work was supported by FIR, project number FS-375-S.

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I. INTRODUCTION

Low levels of nitrogen availablility limit biomass production in many forests of the Pacific Northwest, and considerable interest has been shown in the potential of biological nitrogen fixation (Briggs *et al*., 1978; Gordon *et al*., 1979; Trappe *et al*., 1968). In western Oregon the most important nitrogen fixing plants are red alder (*Alnus rubra* Bong.) and *Ceanothus* species. Some of these species could play an important role in stimulating forest growth, primarily through increases in nitrogen level and secondarily through improved soil physical conditions and increases in other nutrient levels (Wollum and Youngberg, 1964).

Red alder is known as a pioneer species with vigorous juvenile growth, able to grow faster than coniferous associates for the first 15 years (Fowells, 1965). It grows predominantly on moist sites and forms a symbiosis with an actinomycete (*Frankia* sp.) capable of nitrogen fixation. In areas of low soil nitrogen levels red alder could become especially important for improving soil N levels (Tarrant, 1961; Hughes *et al*., 1968; Miller and Murray, 1978; Binkley, 1983). Elemental cycling is faster in alder than in the conifer ecosystems. The higher nitrogen content of red alder litter not only provides for rapid buildup of soil nitrogen but also leads to a more rapid decomposition rate of organic material in the soil and forest floor (Cole *et al*., 1978). Nitrogen accretion and improvement of other soil characteristics induced by red alder suggest opportunities for increasing yields of crop trees grown with red alder.

While red alder grows on moist bottom-land sites, *Ceanothus* species are distributed mainly on drier sites. *Ceanothus* is tolerant of drought and of very infertile sites. Many *Ceanothus* species also form a symbiosis with *Frankia* species. *Ceanothus* occurs in one of two situations. First, it may occur as a regular component of forest communities that lack a closed canopy. Second, it may exist as an early successional species on sites that develop a closed forest canopy (Franklin, 1982). In both situations, *Ceanothus* fixes atmospheric nitrogen at rates which are ecologically significant (Delwiche *et al*., 1965; Binkley *et al*., 1982; McNabb and Cromack, 1983).

Some researchers have examined the effects of *Ceanothus* on associated conifer growth. Tappeiner and Helms (1971) reported higher survival rate of Douglas-fir and white-fir natural regeneration in *C. prostratus* mats than in several other microsites. Other species may respond differently to the presence of *Ceanothus*, however (Zavitkovski *et al*., 1969). Scott (1969) reported that 9-year-old Douglas-fir height was 1.6, 1.2, and 0.8 m under snowbrush canopies, at the edge of the canopies, and in the open, respectively. However, there were no differences in height growth if conifers were dominant relative to the snowbrush canopy (Horowitz, 1980). An effect of Ceanothus on site quality was observed by Youngberg et al. (1979) who found higher foliar nitrogen (1.56 % N) in Douglas-fir seedlings growing under snowbrush than in seedlings growing in the open (1.15 % N) or at the edge of snowbrush canopies (1.32 % N).

Nitrogen fixation, which induces nitrogen accumulation in forest ecosystems, varies according to the environment. Soil nutrients are one of the factors affecting nitrogen fixation. Although high levels of nitrogen cause a negative effect (Rodriguez-Barrueco et al., 1970; Hughes et al., 1968), increased levels of calcium, sulfur, and phosphorus promote nodulation and nitrogen fixation (Scott, 1973; Seiler and McCormick, 1982). The micronutrients, molybdenum, cobalt, and nickel are necessary for nitrogen fixation in legumes and may be required as well by non-leguminous plants (Silvester, 1977).

Moisture, temperature, and light also influence nitrogen fixation (Wollum and Youngberg, 1969; Youngberg et al., 1979; Seiler and Johnson, 1984). Photosynthates produced by the host and transported to the roots supply carbohydrates to the noduler endophyte (Paul and Kucey, 1981). Dawson and Gordon (1979) reported that there were significant correlations between leaf area and acetylene reduction, and between photosynthetic rate and nitrogen content in a nodulated plant. Nitrogen fixing plants compete with regenerating conifers for light, water, and nutrients, which may cause detrimental effects on forest regeneration (Zavitkovski et al., 1969). The net effect of these nitrogen fixing species in conifer plantations is the result of their competitive interaction with crop trees early in plantation development and the nutrient enhancement of the site for the entire rotation.

The effect of stand density on red alder nitrogen fixation was reported by Bormann and Gordon (1984). Nitrogenase specific activity (acetylene reduction per unit nodule dry mass) and average nitrogen fixation per tree decreased as tree density increased. However, nitrogen fixation per unit area appeared to peak at a density of 5,000 trees/ha, and declined at a density of 10,000 trees/ha. Trees growing at a higher density may have reduced foliage relative to their respiratory surface, and thus have less photosynthate available for use by the belowground system. As a forest grows older, density and other factors affecting nitrogen fixation would be changed. Understanding the nitrogen fixing activities for different growing conditions in the field will help to determine the extent of future use of nitrogen fixing plants.

Nitrogen fixation rates can be measured by several methods such as N accretion, chronosequence method, ^{15}N analysis, and acetylene reduction assay. For the N accretion and chronosequence methods, total nitrogen in the

ecosystem is subtracted from an initial nitrogen level in the ecosystem to get the amount of nitrogen accumulated during the growing period. There are many ways of using nitrogen isotopes for the measurement of nitrogen fixation. One of the useful methods is using natural ^{15}N in soil fractions which may be quite different from that in the atmosphere (Delwiche and Steyn, 1970). However, the Acetylene reduction assay, which was used in this study, is much more convenient than the ^{15}N analysis method.
The acetylene reduction assay is cheap, more sensitive than other methods, rapid, and requires little technical skill. There are, however, limitations that should not be overlooked when using doing acetylene reduction assays. The ethylene production in the absence of acetylene should always be tested by using suitable controls. While Hardy et al. (1971) presented good correlations between acetylene reduction and nitrogen fixation, wide variations were found by Bergersen (1970). In many acetylene reduction assays, the theoretical ratio of 3:1 (nitrogen fixation : acetylene reduction) is used to convert acetylene reduction rate to nitrogen fixation rate (Tripp et al., 1979; Binkley, 1981; Bormann and Gordon, 1984). However, it is necessary to check the exact relationship between acetylene reduction and nitrogen fixation for the particular environment under study.

The objectives of this investigation were to determine nitrogen fixation and its role in western Oregon forest ecosystems. To meet the general objectives, the following specific objectives were undertaken: (1) to determine the differences in nitrogen fixing activities of red alder at different ages, (2) to determine the differences in nitrogen fixing activities of various *Ceanothus* species in different locations, and (3) to determine the nitrogen fixation rates and the amount of nitrogen input by these nitrogen fixing plants in western Oregon forest ecosystems.

II. NITROGEN FIXATION OF RED ALDER IN WESTERN OREGON

SITE DESCRIPTIONS

Red alder samples were collected from the Cascade Head Experimental Forest, the Alsea Ranger District of the Siuslaw National Forest, and the OSU Field Laboratory. Table 1 provides a summary of site descriptions.

Csacade Head Experimental Forest is located 5 miles from the coast and about 2 miles north of Otis, Oregon. The area lies within the "fog belt". A marine climate provides equitable temperatures, much cloudiness, frequent rain, and summer fog (Madison, 1957). The stand was once cleared for agriculture but was abandoned about 1925. A 1-acre plot containing about 3,000 trees per acre, of which 60 percent were conifer (Douglas-fir 12 %, Sitka spruce 43 %, western hemlock 5 %) and 40 percent were alder, was established in 1935 (Berntsen, 1961). As a 58-year-old stand the density decreased to 620 trees per acre but had the same percentage of conifers and alder. Site index of this area is 37 m at 50 years for Douglas-fir (Binkley and Green, 1983).

The site at the Alsea Ranger District of the Siuslaw National forest is located 12 miles southwest of Alsea, Oregon. A previous old-growth Douglas-fir stand at the site was clearcut and slash burned around 1982-1983. One-year-old red alder seedlings were planted in 1984 using a Nelder design (Nelder, 1963) with three replications.

After one year, dead seedlings were replaced by other one-year-old seedlings. Vine maple is a major competing shrub species on the established plots. Average annual precipitation is 214 cm and the weather is fairly dry during July and August.

The OSU Field Laboratory is located one mile east of Corvallis, Oregon. Soil was formed on recent alluvial flood plains and has a loamy texture in the upper 20 inches. Average precipitation on this site is 108 cm/yr. However, the precipitation of 69 cm/yr in 1985 was the lowest since 1944 (Redmond, 1986). In 1984, one-year-old red alder seedlings were planted on the site, which previously had been under cultivation with various annual crop species.

Table 1. Descriptions of alder sites

Site	Elevation	Latitude	Slope	Aspect	Climate	Soil
	(m)	(North)	(%)			
Cascade Head	180	45°3'	15	SW	average ppt.: 240 cm/yr mean annual temperature: 10°C	Haplumbrepts, well drained silty clay loam developed from deeply weathered siltstone
Alsea	250	44°11'	0	-	average ppt.: 214 cm/yr	Haplumbrepts, well drained loam to silty clay loam formed in residuum and minor colluvium derived from micaceous sandstone with thin siltstone interbeds
OSU Field Laboratory	210	44°34'	0	-	average ppt.: 108 cm/yr mean annual temperature: 11°C	Haploxerolls, loam developed from recent alluvial flood plains

MATERIALS AND METHODS

Nitrogen fixation rates of red alder were measured using the nodules of 2-year-old and 58-year-old trees. Six well distributed larger young trees from the Alsea site and three from the OSU Field Laboratory were used for each set of measurements. To determine seasonal nitrogen fixation, each set of 12 to 18 nodule samples was collected monthly from April to October in 1985. Nodule samples of old red alder at the Cascade Head Experimental Forest were taken on a 1 x 1 m areal basis because the root system of the larger trees could not be separated. Six 1 x 1 m soil pits with a depth of 30 cm were digged every month and nodule samples were excavated from the soil pits. Each set of 12 to 18 nodule samples was collected monthly from April to November in 1985. Procedures for assessment of nitrogen fixation (except for gas analysis) were performed in the field.

The intact nodules with roots trimmed to within 1 cm of the nodules were placed in a bottle. Fifty-ml bottles were used for the nodules of young red alder and 500-ml bottles for the nodules of old red alder. Some soil around the nodules was added to the bottle to maintain in situ moisture. Total volume of the nodules and soil was kept at no more than one-third of the container volume. The air of ten percent of the volume of the bottle was removed and replaced with an equal amount of acetylene gas to make an atmosphere of ten percent acetylene. Then the bottle was located at an appropriate depth to maintain in situ temperature. After one hour of incubation, a gas sample was transferred to a 10-ml vacutainer tube and stored until analyzed (Stutz and Bliss, 1973; McNabb and Geist, 1979). Each set of measurements has a nodule blank and a soil blank to check the amount of ethylene gas evolved without adding acetylene gas.

Subsamples from the vacutainer tubes were analyzed on a gas chromatograph (Hewlett Packard Model 5830A) with a flame ionization detecter and a column packed with Porapak R, 80-100 mesh. The concentrations of acetylene and ethylene gas in the subsamples were interpreted by a gas chromatograph terminal (Hewlett Packard Model 18850A). Acetylene reduction rates were calculated by using an ideal gas law, $n = PV/RT$ and the relationship between the moles of acetylene and ethylene (McNabb and Geist, 1979). The data are plotted as µmoles of ethylene produced.

The nodule samples used for acetylene reduction measurements were removed from the roots and washed with water to dislodge soil particles, then dried at 70 ^{o}C for two days. Nodule dry weights were used to estimate acetylene reduction rates.

Twelve trees at the Alsea site were selected randomly for the measurements of tree height, basal diameter, crown width, leaf dry weight, stem dry weight, root dry weight, and nodule dry weight. The samples were collected in September 1985 and dried at 70 ^{o}C for two days. A statistical relationship between nodule biomass and tree aboveground dimensions was evaluated by regression analysis. Nodule biomass per tree was obtained from this relationship and converted to the nodule biomass per unit area by a stand density of 10,000 trees/ha which was assumed because red alder seedlings about 1 m apart were mainly used for the measurement of nitrogen fixation. Nodule biomass of old red alder at Cascade Head was calculated directly from the dry weights of nodules which were collected on an areal basis.

Acetylene reduction rates were converted to nitrogen fixation rates by a conversion factor of 3, assuming 1 mole of nitrogen fixation for 3 moles of acetylene reduced (Hardy _et_ _al_., 1973). Growing period was estimated from the number of months when the nodules were significantly active. Nitrogen fixation rates were calculated by the following equation:

$$N = \frac{A}{C} \times B \times H \times M \times 10^{-6}$$

where N : Nitrogen fixation rate (kg/ha/yr)
A : Acetylene reduction rate (μmole/g/hr)
C : Conversion factor
B : Nodule biomass (kg/ha)
H : growing period (hr/yr)
M : Nitrogen molecular weight (g/mole)

Analysis of plant nitrogen was obtained from the samples of leaf, stem, twig, root, and nodule collected from each of five trees at the Alsea site and OSU Field Laboratory. At Cascade Head, leaf, nodule, and litter samples were collected from five 1 x 1 m soil pits. The samples were oven-dried at 70 °C for two days. Total nitrogen in each plant part was determined using the Kjeldahl method by the Soil Testing Laboratory at Oregon State Univesity.

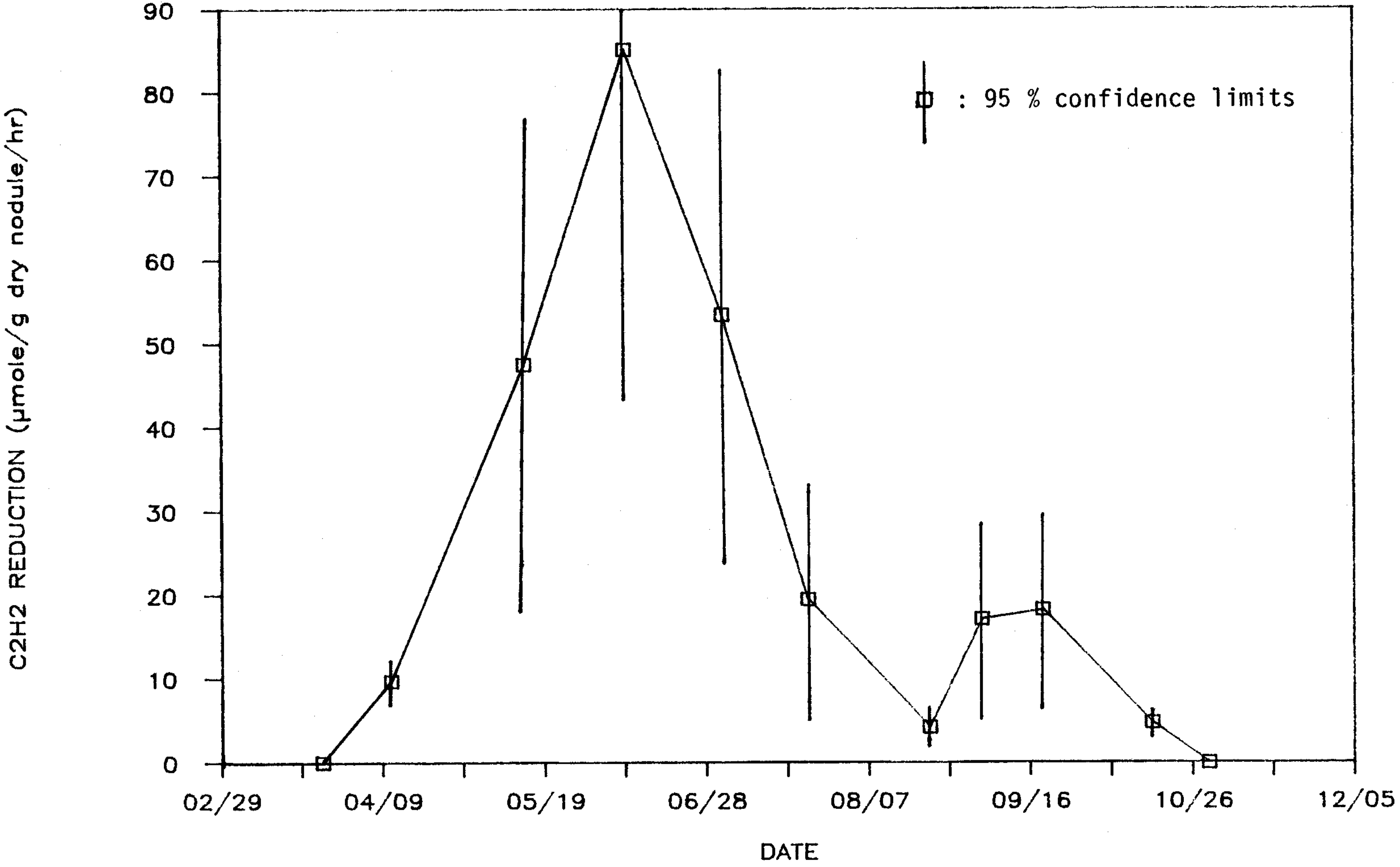
RESULTS

Annual acetylene reduction

Seasonal pattern of acetylene reduction by 2-year-old red alder at the Alsea site is shown in Figure 1. The values represent the average of 6 to 10 samples at each sampling date. The 95 percent confidence limits are also plotted. From the measurements on a sampling date, the samples collected between 10:00 and 11:30 a.m. were used as a daily mean. The maximum acetylene reduction rate of 85.1 µmole/g dry nodule/hr occurred in June. During the months of July and August, the rate dropped sharply to 4 µmole/g dry nodule/hr. The activity increased to 18.3 µmole/g dry nodule/hr after rainfall started in early September, and finally decreased to a nontetectable level in November. Considerable variation in the activity on each sampling date is evident in Figure 1. Greatest variability occurred in May and July when the 95 percent confidence limits were approximately 70 percent of the mean. During the months of June, August, and September, the confidence limits were 50 to 60 percent of the mean. In April, the confidence limits were about 30 percent of the mean, and in October they were 14 percent. The average acetylene reduction rate during a growing season was 29.4 µmole/g dry nodule/hr for the Alsea site.

Seasonal pattern of acetylene reduction at the OSU Field Laboratory was somewhat different from that at the

Figure 1. Seasonal pattern of acetylene reduction by 2-year-old red alder at the Alsea site



Alsea site (Figure 2). The maximum acetylene reduction rate occurred in May (52.4 μmole/g dry nodule/hr). The rate dropped to 18.5 μmole/g dry nodule/hr in June and declined further to 6.4 μmole/g dry nodule in early September. After the activity recovered with rainfall in September, it fluctuated from 3.8 to 14.2 μmole/g dry nodule/hr until November. Variation in activity was greatest in June when the 95 percent confidence limits were 90 percent of the mean. In May, it was about 50 percent. The confidence limits for the remaining months were about 30 percent of the mean. The average acetylene reduction rate of 2-year-old red alder during a growing season was 22.0 μmole/g dry nodule/hr at the OSU Field Laboratory.

Seosonal pattern of acetylene reduction by 58-year-old red alder at the Cascade Head Experimental Forest was quite different from that at the Alsea site and the OSU Field Laboratory (Figure 3). The activity reached a maximum level in May and maintained the same level throughout October. Maximum rate occurred in July (10.2 μmole/g dry nodule/hr). The variation in activity was greatest in May when the 95 percent confidence limits were about 90 percent of the mean. In April, It was about 70 percent. The confidence limits from July to October fluctuated from 50 to 60 percent of the mean. The average acetylene reduction rate of 58-year-old red alder during a growing season was 8.5 μmole/g dry nodule/hr for the Cascade Head Experimental Forest.

Figure 2. Seasonal pattern of acetylene reduction by 2-year-old red alder at the OSU Field Laboratory

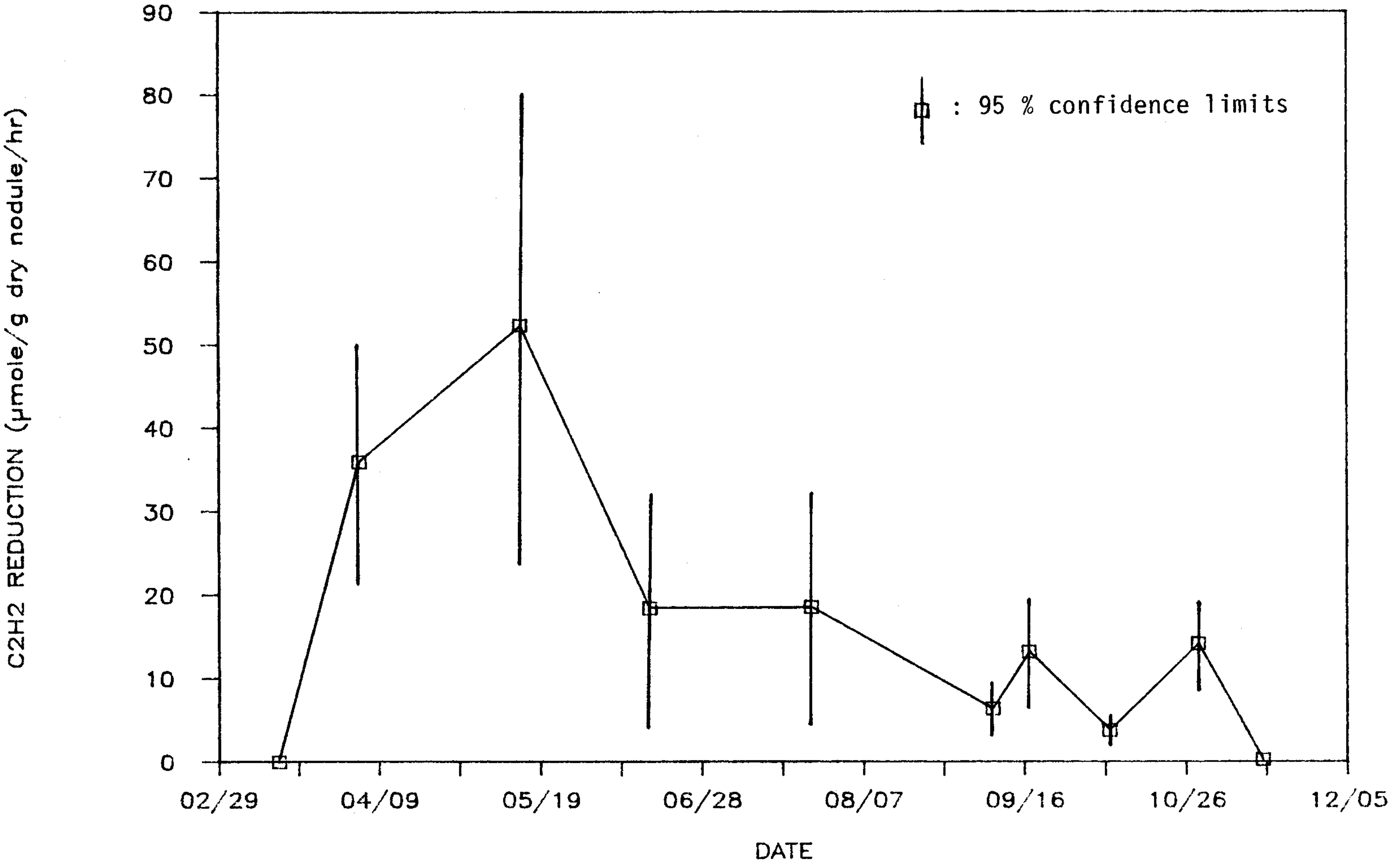
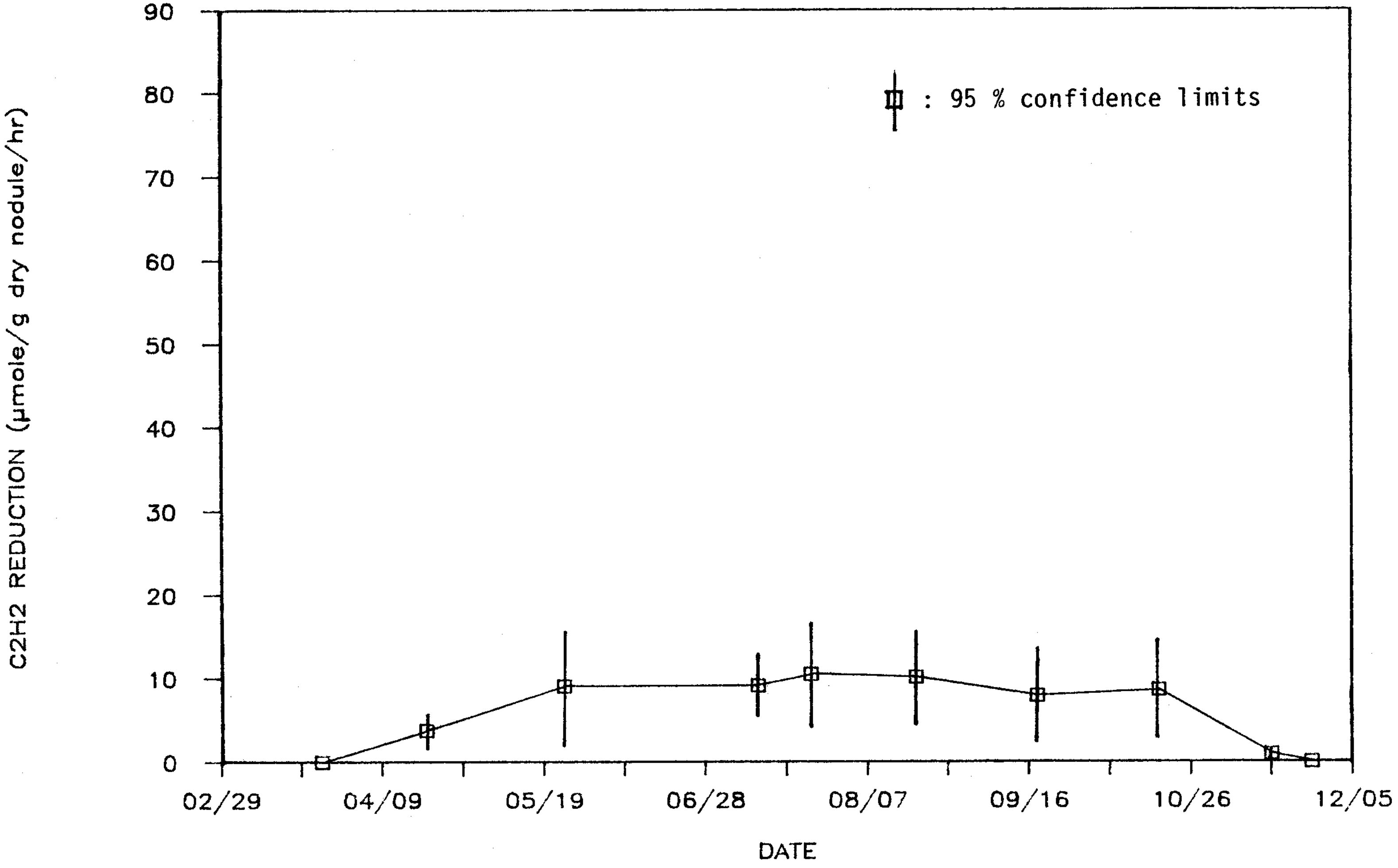


Figure 3. Seasonal pattern of acetylene reduction by 58-year-old red alder at the Cascade Head Experimental Forest



Soil temperature at the OSU Field Laboratory increased from 8.2 °C to 15.4 °C during the months of April and May, while it increased from 7.0 °C to 9.0 °C at the Alsea site during the same period (Figure 4).

Nodule biomass

Nodule biomass of 2-year-old red alder was estimated by the following equation:

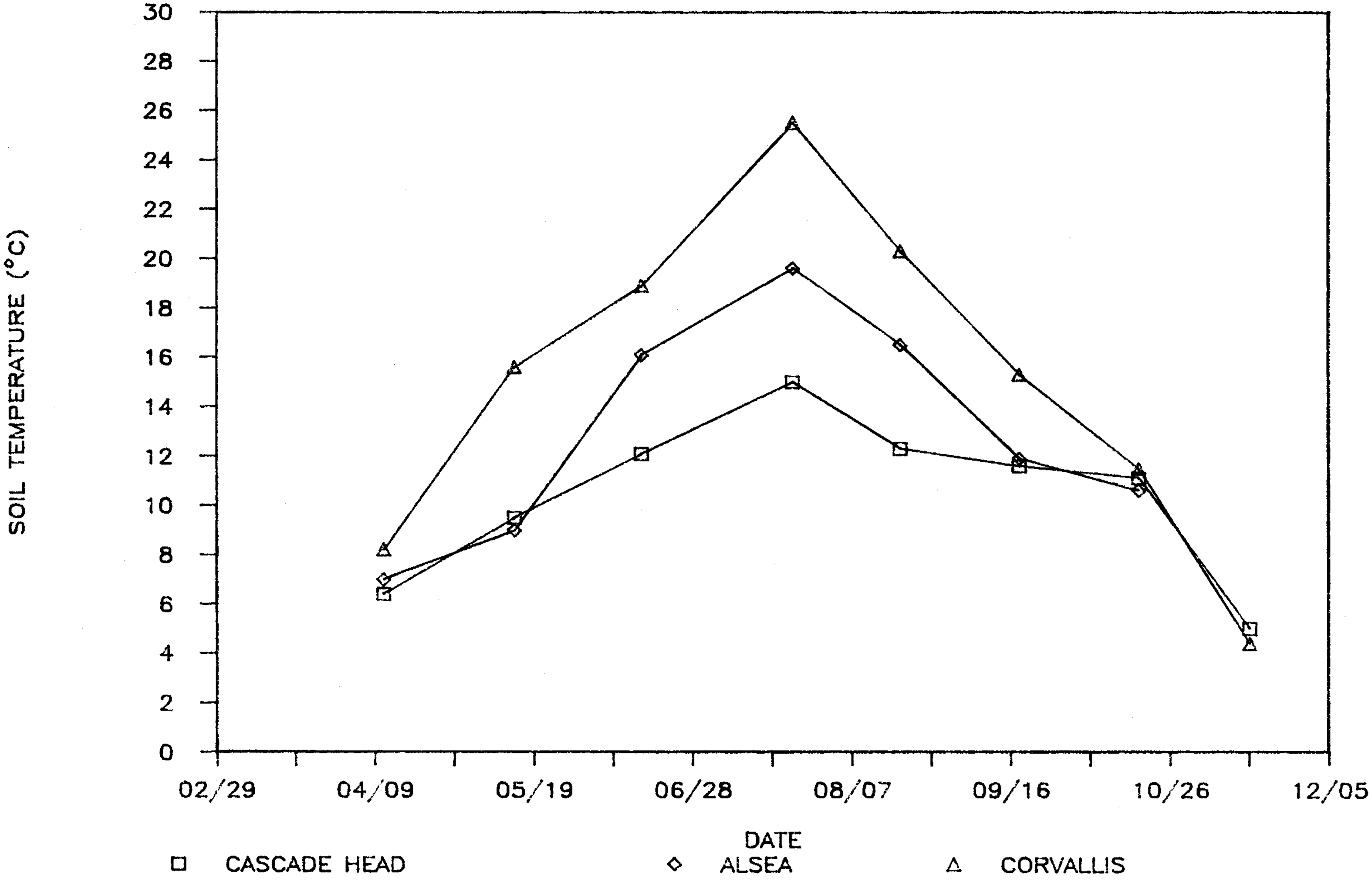
$$Y = -0.307 + 0.021X_1 + 0.006X_2 - 0.028X_3 \quad (R^2 = 0.932)$$

where Y : Nodule dry weight (g)
X_1: Tree height (cm)
X_2: Basal diameter square (mm^2)
X_3: Crown width (cm)

R^2: Adjusted R^2 ($n = 12$)

The average nodule biomass of 2-year-old red alder at the Alsea site was 1.63 g/plant and 16.29 kg/ha, assuming stand density of 10,000 trees/ha. Nodules of 58-year-old red alder were different from those of young red alder primarily by size. The largest nodules at Cascade Head were 4.5 inches in diameter and less than one half inch for young nodules at the Alsea site. The large nodules from Cascade Head had inactive nodule material of average about 35 percent by weight. The inactive nodules were separated by their darker color and decayed inner component. Nodule biomass of 58-year-old red alder at Cascade Head, measured on an areal basis, was 93.24 kg/ha (Table 2). The values include only nodules in the upper 30 cm of soil. Two of

Figure 4. Soil temperature at alder sites (15-30 cm depth)



six soil pits had a few large nodules below 30 cm depth, which averaged about 30 percent of the nodule biomass within the upper 30 cm of the soil. The estimated additional 30 percent or more may exist in layers below the 30 cm depth, for a total of about 121 kg/ha of nodules at the site.

Nitrogen fixation

Annual nitrogen fixation was estimated by the sum of monthly nitrogen fixation rates, which were converted from monthly acetylene reduction rates. The estimated annual nitrogen fixation was 22.79 kg N/ha/yr, 17.51 kg N/ha/yr, and 50.11 kg N/ha/yr for the Alsea site, the OSU Field Laboratory, and the Cascade Head Experimental Forest, respectively (Table 3).

Nitrogen analysis

Nitrogen concentrations for the plant parts are shown in Table 4. Values represent the average of 12 samples collected from the Alsea site and the average of 3 samples from the OSU Field Laboratory and the Cascade Head Experimental Forest. Nitrogen concentrations of young red alder were similar to those of old red alder, with higher values in leaves and nodules. Nitrogen concentration of nodules at the OSU Field Laboratory was significantly lower than those at other sites. Nitrogen concentration of

Table 2. Nodule biomass of 58-year-old red alder at the Cascade Head Experimental Forest

Date	Soil pit	Active nodule	Inactive nodule	Total nodule	Nodule[a] biomass	Inactive nodule
		g/m^2	g/m^2	g/m^2	kg/ha	%
JUL 12	5	5.20	2.63	7.83	78.34	33.6
JUL 25	7	4.53	1.50	6.03	60.29	24.9
AUG 20	5	10.84	10.59	21.43	214.32	49.4
SEP 19	5	3.10	1.16	4.26	42.58	27.2
OCT 19	5	2.81	1.83	4.64	46.44	39.6
NOV 16	3	10.23	1.52	11.75	117.50	12.9
Average					93.24 (±26.65)[b]	31.3

[a] Nodules of upper 30 cm of soil.

[b] Standard error.

Table 3. Estimates of nitrogen fixation by red alder in western Oregon

Location	Age	Alder density	C2H2[a] reduction	Nodule biomass	Growth period	Nitrogen fixation
	yrs.	#/ha	µmole/g/hr	kg/ha	months	kg/ha/yr
Cascade Head	58	588	7.54	121	8	50.11
Alsea	2	10,000	29.38	16.29	7	22.79
OSU Field Lab.	2	10,000	22.01	16.29[b]	7	17.51

[a] Mean annual acetylene reduction.

[b] Nodule biomass is assumed to be same as at Alsea.

litter at Cascade Head Experimental Forest was less than that of fresh material by 0.3 to 0.4 percent. Inactive nodules had 0.25 percent less nitrogen than active nodules. Leaf nitrogen in 2-year-old red alder was about 45 percent of the total tree nitrogen.

Table 4. Nitrogen analysis of red alder

	Leaf	Stem	Twig	Root	Nodule	Total
Nitrogen concentration (%)						
Alsea	2.48^a	0.69^a	0.98^a	0.87^a	2.33^a	
OSU Field Lab.	2.62^a	0.59^a	0.91^a	0.83^a	1.77^b	
Cascade Head	2.27^a (1.84)*	-	- (0.56)*	-	2.38^a (2.13)**	
Biomass at the Alsea site (g/tree)						
	27.41	35.68	28.57	34.29	1.63	127.58
Nitrogen content at the Alsea site (g/tree)						
	0.680	0.246	0.280	0.298	0.038	1.542

[a,b] Tukey's procedure (5 % significance level).

* Nitrogen concentration of litter at Cascade Head.

** Nitrogen concentration of inactive nodules at Cascade Head.

DISCUSSION

At the Alsea site and at the OSU Field Laboratory, the maximum rate of acetylene reduction by 2-year-old red alder occurred at midday except during the months of summer drought. Wheeler (1969) observed maximal rates of nitrogen fixation by one-year-old _Alnus glutinosa_ at about midday. Tripp _et al_. (1979) found that the maximum rate occurred at midday in 2- and 3-year-old red alder, with midday rates being four to six times greater than night rates. In this study, sampling time was chosen between midmorning and noon for the Alsea site and the OSU Field Laboratory, assuming that the rate was at the daily mean at that time. At Cascade Head, however, diurnal variation of acetylene reduction was not evident and samples were collected at 1 to 2 hour intervals during the daytime.

During the months of April and May, acetylene reduction activity of 2-year-old red alder was higher at the OSU Field Laboratory than at the Alsea site. It seems that the earlier high activity at the OSU Field Laboratory was due to the higher soil temperature. Soil temperature at the OSU Field Laboratory increased 7.2 ^{o}C during the months of April and May, while it increased only 2.0 ^{o}C at the Alsea site during the same period (Figure 4). Wheeler (1971) reported that _Alnus glutinosa_ reached maximum acetylene reduction at about 25 ^{o}C, and, at this temperature, the reaction was six times faster than at 15 ^{o}C.

The acetylene reduction activity started to decrease earlier at the OSU Field Laboratory than at the Alsea site. Moisture stress seems to be a main reason for the early rate decrease at the OSU Field Laboratory. During the months of January to June in 1985, precipitation was 13.05 inches and 29.15 inches for the OSU Field Laboratory and the Alsea site, respectively (Figure 5). Soil moisture content at the Alsea site and the OSU Field Laboratory in May and June are shown in Table 5. Seiler and Johnson (1984) found from *Alnus glutinosa* that acetylene reduction rates decreased only slightly in the range of water potentials from -0.50 to -1.29 MPa, then dropped rapidly below water potentials of -1.30 MPa. The precipitation and soil moisture content data suggest that there was more moisture stress at the OSU Field Laboratory than at the Alsea site in May and June.

Table 5. Soil moisture content at the Alsea site and the OSU Field Laboratory*

	Alsea $\bar{X} \pm SE$	OSU Field Laboratory[a] $\bar{X} \pm SE$
	% (g/g)	% (v/v)
APR	N.D.**	48.7 ± 2.0
MAY	54.1 ± 1.9	43.1 ± 0.6
JUN	36.0 ± 0.7	N.D.
JUL	N.D.	34.6 ± 1.0
AUG	33.6 ± 1.6[b]	34.3 ± 0.8
SEP	N.D.	33.4 ± 0.2

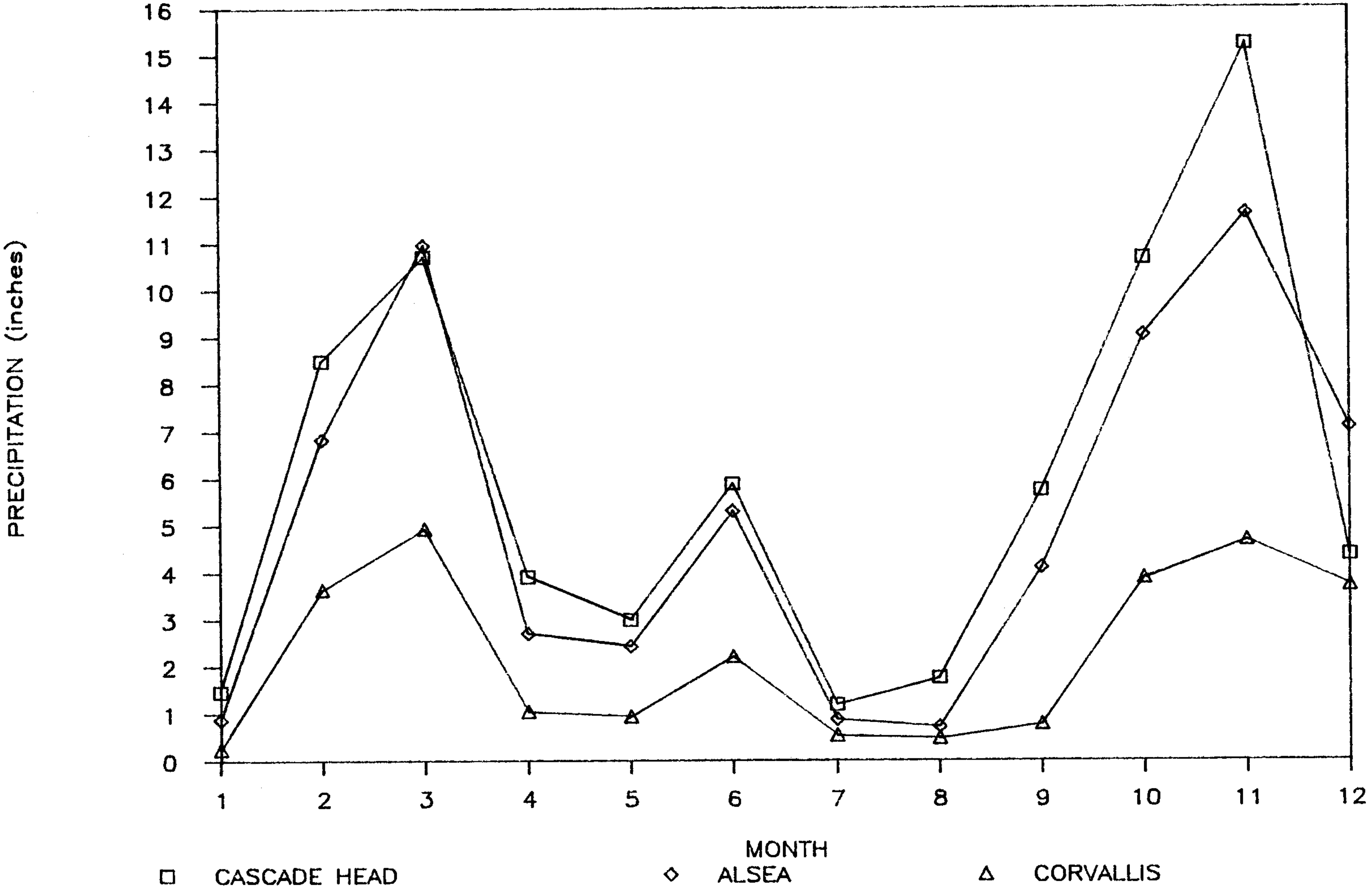
* Samples were collected from upper 30 cm of soil.

** N.D.: not measured.

[a] L. Shainsky, unpublished data.

[b] D. Hibbs, unpublished data.

Figure 5. Precipitation at alder sites in 1985



Seasonal patterns of acetylene reduction by 2-year-old red alder at both sites correspond with the report of Tripp _et al_. (1979), except for the months of July and August. During those months, the rate dropped sharply in the current study, which might have been caused by the summer drought. Plant moisture stress at the Alsea site is shown in Table 6. Predawn xylem pressure potential at the OSU Field Laboratory was -0.2 to -0.3 MPa in May and -0.6 to -0.7 MPa in early September in 1986 (L. Shainsky, unpublished data). Cromack _et al_. (1979) also observed a decrease in acetylene reduction rates from a snowbrush stand in the western Cascades during the same period. Acetylene reduction in 2-year-old red alder was evident during the growing season starting in April and continuing into October. In February, 1986, the rate was 0.0024 µmole/g dry nodule/hr, which was almost negligible.

Table 6. Xylem pressure potential at the Alsea site[*]

(1985)	Predawn $\bar{X} \pm$ SE	Midday $\bar{X} \pm$ SE
	MPa	MPa
JUN 12[a]	-0.25 ± 0.02	-1.28 ± 0.02
AUG 25[b]	-0.46 ∓ 0.05	-1.42 ∓ 0.02

[*] D. Hibbs, unpublished data.
[a] n = 32.
[b] n = 33.

Acetylene reduction rates of 58-year-old red alder were lower than the rates of 2-year-old red alder, and not much changed through the growing season. The greater precipitation together with a stable growth environment at Cascade Head might have contributed to the steady activity of acetylene reduction there. Soil nitrogen level at Cascade Head was 4 to 6 times higher than the level at the Alsea site and OSU Field Laboratory, which might have been unfavorable for nitrogen fixation at Cascade Head (Table 7). The lower soil temperature (maximum of 15 °C in July) at Cascade Head also might have contributed to the low acetylene reduction activity. In February, the activity of old red alder was also negligible at 0.004 µmole/g dry nodule/hr.

The values of estimated nodule biomass at the Cascade Head and Alsea sites were compared with the values obtained by other investigators listed in Table 8. Nodule biomass of 58-year-old red alder is relatively lower than other values, and nodule biomass of 2-year-old red alder at the Alsea site is the lowest of the values in Table 8.

Table 7. Soil N and C at red alder sites
(upper 30 cm of soil)

	Soil N $\bar{X}$ ± SE	Soil C $\bar{X}$ ± SE	C/N ratio $\bar{X}$ ± SE
	ppm	ppm	
Cascade Head[a]	6,450 ± 800	145,125 ± 19,350	23 ± 3
Alsea site[b]	1,499 ± 120	49,771 ± 4,945	37 ± 4
OSU Field Lab.[c]	1,020 ± 36	18,475 ± 822	18 ± 1

[a] Franklin *et al.*, 1968.
[b] D. Hibbs, *unpublished* data.
[c] Sampled in July, 1985 (n = 6).

Table 8. Estimated nodule biomass of alder

Nodule biomass	Stand	Age	Reference
kg/ha		yrs.	
117	red alder	7	Zavitkovski and Newton 1968
244	red alder	30	"
146	red alder (4,000/ha)	5	Bormann and Gordon 1984
62	red alder (10,000/ha)	5	"
390	red alder/ Douglas-fir	15-20	Binkley 1981
110	Sitka alder/ Douglas-fir	15-20	"
130	Sitka alder	5	Binkley 1982
454	black alder	5-20	Akkermans and Van Dijk 1976
16	red alder	2	This study
121	red alder/ conifer	58	This study

The nitrogen fixation rate estimated from mean annual acetylene reduction was 0.27 mg N/g dry nodule/hr and 0.21 mg N/g dry nodule/hr at the Alsea site and the OSU Field Laboratory, respectively. Those rates are comparable to a rate of 0.26 mg N/g dry nodule/hr for red alder obtained by Tripp _et_ _al_. (1979). The nitrogen fixation rate of old red alder at Cascade Head was estimated at 0.07 mg N/g dry nodule/hr, showing lower nitrogen fixation than those of young red alder. Nevertheless, annual nitrogen fixation at Cascade Head was more than two times the amount at the other sites because of the greater nodule biomass (Table 3).

Annual nitrogen fixation in this study is compared with estimates of other workers in Table 9. Annual nitrogen fixation of 2-year-old red alder in the present study was lower than the estimates of the other researchers. However, the estimated 23 kg/ha/yr and 18 kg/ha/yr of nitrogen inputs by 2-year-old red alder are still substantial, and will be greater in the future. Miller and Murray (1979) estimated that a nitrogen fixation rate of 20-50 kg/ha/yr might be sufficient to alleviate nitrogen deficiency for the growth of Douglas-fir. In natural, even-aged stands, Douglas-fir dominates red alder at or before age 30 (Miller and Murray, 1978). The 58-year-old mixed stand of red alder and conifers growing at Cascade Head still showed the potential for substantial nitrogen input, which was 50.1 kg/ha/yr.

Table 9. Estimates of annual nitrogen fixation in red alder ecosystems

Annual N fixation (kg/ha/yr)	Location	Soil fertility	Age (yrs.)	Component	Reference
(Pure stands)					
320	Oregon, Coast Range	N deficient	2-15	Biomass + top[a] 60 cm of soil	Newton et al. 1968
80	Washington	-	0-4	Soil to 15 cm[a]	DeBell and Radwan 1979
85	Western Washington	-	0-38	Ecosystem[a]	Cole et al. 1978
50	Washington	Site index 50 m (100yr)	10-40	Forest floor +[a] soil to 20 cm	Bormann and DeBell 1981
100+	Washington	Site index 50 m (100yr)	10-40	Forest floor +[a] soil to 50 cm	"
100	Greenhouse	-	1	Ecosystem[b]	Zavitkovski and Newton 1968
140	Greenhouse	Total soil N 110 ppm	7	Ecosystem[b]	"
209	Greenhouse	Total soil N 310 ppm	30	Ecosystem[b]	"
62	Washington	Total soil N 300 ppm	2-4	Ecosystem[c]	Tripp et al. 1979

Table 9. (Continued)

Annual N fixation (kg/ha/yr)	Location	Soil fertility	Age (yrs.)	Component	Reference
70	Northwestern Oregon	Site class II	5	Ecosystem[c]	Bormann and Gordon 1984
23	Oregon, Coast Range	-	2	Ecosystem[c]	This study
18	Western Oregon	-	2	Ecosystem[c]	This study
(With Douglas-fir)					
40	Southwestern Washington	-	0-26	Soil to 90 cm[a]	Tarrant and Miller 1963
13	Oregon, Coast Range	-	0-17	Soil to 15 cm[a]	Berg and Doerksen 1975
51	Oregon Coast Range	-	0-17	Soil to 15 cm[a]	"
65	British Columbia	Site index 24 m (50 yr)	0-23	Soil to 50 cm[a] + biomass	Binkley 1982
42	Northwestern Washington	Site index 45 m (50 yr)	0-23	Soil to 50 cm[a] + biomass	"

Table 9. (Continued)

Annual N fixation (kg/ha/yr)	Location	Soil fertility	Age (yrs.)	Component	Reference
130	British Columbia	Site index 24 m (50 yr)	15-20	Ecosystem[c]	Binkley 1981
50	Oregon, Coast Range	Site index 37 m (50 yr)	58	Ecosystem[c]	This study
(With cottonwood)					
32	Washington	-	0-4	Soil to 15 cm[a]	DeBell and Bormann 1979

[a] Based on accretion studies.

[b] Based on greenhouse accretion per gram of nodule.

[c] Based on acetylene reduction assays.

The higher nitrogen concentration and approximately 45 percent of total plant nitrogen in leaves of young red alder indicate that nitrogen demand of young red alder is predominantly for leaf production. The rapid decomposition of organic material and rapid elemental cycling in red alder ecosystems (Cole _et al_., 1978) might be supported by the higher nitrogen content in leaves of red alder. Elements such as N and P as well as carbon substrate quality would influence red alder decomposition and the recycling of these elements, based upon hypotheses advanced by Berg (1986) and by McClaugherty and Berg (1987).

The nitrogen supplying effect of red alder can be expected from 2 years of age if red alder is maintained at high density. Red alder can supply substantial nitrogen even at 58 years of age when it is overtopped by associated conifers. With high costs of nitrogen fertilizer, red alder will probably play an important role in forest management. By maintaining sufficient red alder density, substantial nitrogen will be supplied continuously to the ecosystem.

The dynamics of fixed nitrogen in the red alder ecosystem should be determined for a better understanding of the nitrogen supplying effect of red alder.

III. NITROGEN FIXATION OF *Ceanothus* SPECIES IN SOUTHWESTERN OREGON

SITE DESCRIPTIONS

Two study sites were located on the Siskiyou National Forest of the Klamath Mountains in southwestern Oregon. A summary of site descriptions is shown in Table 10.

The first site is located near Waters Creek, 3 miles north of Wonder, Oregon. The site is in the Mixed-Conifer Zone (Franklin and Dyrness, 1973). *C. velutinus* is important as a brushfield dominant or invader following logging or fire in this zone. Average elevation of the site is 540 m on a 60 percent, north facing slope. The previous Douglas-fir stand was clearcut, and piled and burned in 1980. Douglas-fir seedlings were replanted in 1981. Today, dense patches of 5- to 6-year-old varnishleaf (*C. velutinus* var. *laevigatus* (Hook.) T. & G.) have developed on the site with a density of 24,000 shrubs/ha. The shrub height was 1 to 2 m. Some deerbrush (*C. integerrimus* H. & A.) shrubs were scattered among and within the varnishleaf patches. There were also Pacific madrone (*Arbutus menziesii* Pursh) and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) as major competing species. This site has a mesic soil temperature regime and the weather is very dry from July through early September. Average precipitation is 110 cm/yr.

The second site is located near Windy Creek, 4 miles northwest of the Oregon Caves National Monument. It is in the *Abies concolor* zone (Franklin and Dyrness, 1973). *Abies concolor*/*C. velutinus* communities appear in this zone. Average elevation is 1,380 m on a 40 percent, southwest slope. This site has environmental features of lower temperature, less plant moisture stress, and less soil drought than on the Waters Creek site. The old-growth stand was clearcut in 1975, unmerchantable material yarded, and the site burned in 1976. An 11-year-old snowbrush (*C. velutinus* var. *velutinus* Dougl. Ex Hook.) stand has developed on the site with a density of 3,360 shrubs/ha. The shrub height was 1.5 to 2.5 m. Whiteleaf manzanita (*Arctostaphylos viscida* Parry) was a major competing species on the site. Average precipitation is 152 cm/yr. In July 1986, the whole stand was defoliated by an attack of California tortoise-shell butterfly (*Nymphalis california* (Boisduval)), which is noted for occasional vast migratory movements and population "explosions" (Dornfeld, 1980). New leaves emerged in August and the leaves were almost recovered by October. One of the unattacked stands adjacent to the attacked stand was selected as an additional study site to determine the effect of defoliation on nitrogen fixing activity.

Table 10. Descriptions of *Ceanothus* sites

Site	Elevation	Latitude	Slope	Aspect	Climate	Soil
	(m)	(North)	(%)			
Waters Creek	540	42°25'	60	N	average ppt.: 110 cm/yr mean annual temperature: 9°C	Xerochrepts, deep, well drained gravelly loam to gravelly clay loam formed in colluvium and residuum derived dominantly from altered sedimentary and extrusive igneous rock
Windy Creek	1380	42°8'	40	SW	average ppt.: 152 cm/yr mean annual 6.1°C	Xerumbrepts, deep, well drained sandy loam formed in colluvium derived dominantly from granitic rock

MATERIALS AND METHODS

Nitrogen fixation rates were measured using 5- to 6-year-old varnishleaf and deerbrush shrubs at the Waters Creek site and 11-year-old snowbrush shrubs at the Windy Creek site. Two 75 m transects were located at the Waters Creek site, parallel to each other, 20 m apart, and directed to the north. Five 3 x 3 m plots were established at 15 m intervals along each transect. Twelve varnishleaf shrubs of about average size were chosen from the plots for each set of acetylene reduction measurements. Six deerbrush shrubs were chosen from the entire site for each set of measurements because of their infrequent appearance inside the plots. At the Windy Creek site, a 25 m transect was located on the downslope. Five 2.5 x 5 m plots were established at 5 m intervals along the transect. Five snowbrush shrubs were randomly selected from the plots on each sampling date and 12 nodule samples were collected from the shrubs.

To determine seasonal nitrogen fixation, the nitrogenase specific activities of all three species were measured monthly from April through October during 1986. A total of 12 to 18 nodule samples were collected for each species on each sampling date. The procedure of acetylene reduction assay was the same as that for the red alder study in Chapter II. The diurnal acetylene reduction rate was measured for deerbrush in June, July, and August. Three deerbrush shrubs on the site were selected at 2- to

4-hour intervals during a 24 hour period and 3 to 6 nodule samples were collected for each sampling time.

To estimate the statistical relationship between nodule biomass and total aboveground biomass, twenty each of varnishleaf and deerbrush were chosen from the plots at the Waters Creek site. The leaves, stems, and nodules were separated and dried at 70 °C for two days. Regression analysis was used to obtain an equation for predicting nodule biomass using total aboveground biomass. Stem diameters at 8 cm above the ground were measured for all the stems in the plots at the Waters Creek and Windy Creek sites. Total aboveground biomass, leaf biomass, and stem biomass were calculated by the equations given in Table 11. Nodule biomass of varnishleaf and deerbrush was predicted from the mean nodule biomass of ten plots. Five snowbrush

Table 11. Linear regression of varnishleaf and deerbrush biomass components as a function of stem diameter*

Species	dependent variable	Equation**	Adjusted R^2
CEVEL[a]	leaf biomass	$(\ln)Y = -1.370 + 1.770(\ln)X$	0.85
	stem biomass	$(\ln)Y = -2.886 + 2.756(\ln)X$	0.99
	total biomass	$(\ln)Y = -1.908 + 2.527(\ln)X$	0.99
CEIN[b]	leaf biomass	$(\ln)Y = -2.371 + 1.813(\ln)X$	0.86
	stem biomass	$(\ln)Y = -2.605 + 2.630(\ln)X$	0.97
	total biomass	$(\ln)Y = -2.183 + 2.532(\ln)X$	0.97

* Hughes _et al._, in press.

** X is _stem diameter_ (mm) measured 8 cm above the ground for individual stems.

[a] CEVEL = varnishleaf.

[b] CEIN = deerbrush.

shrubs in the plots at the Windy Creek site were selected for a biomass assay. Nodule, stem, and leaf samples were collected in July 1986, and dried at 70 °C for two days. Field weight was converted to an oven-dry weight based on the moisture content of oven-dried plant samples. Biomass of snowbrush at the Windy Creek site was estimated from the mean biomass of the five shrubs. The snowbrush crown was assumed to be 100 percent closed on the site.

Acetylene reduction rates were converted to nitrogen fixation rates by the same procedure as in the red alder study in Chapter II. Annual nitrogen fixation was estimated by the integration of the monthly acetylene reduction and the estimated nodule biomass.

Six shrubs of each species were chosen for nutrient analysis. Stem, leaf, root, and nodule samples were collected from the trees and dried at 70 °C for two days. Plant nitrogen was analyzed by the Kjeldahl method. The other nutrients were analyzed by a Jarrell-Ash ICAP-9000 spectrometer by the Plant Analysis Laboratory, Oregon State University.

RESULTS

Annual acetylene reduction

The seasonal pattern of acetylene reduction by 5- to 6-year-old varnishleaf shrubs at the Waters Creek site is shown in Figure 6. The values represent the average for 12 to 18 samples at each sampling date. The 95 percent confidence limits are also plotted. Acetylene reduction of varnishleaf occurred mainly from April through August. Maximum rate occurred in June at 16.4 µmole/g dry nodule/hr. The rate dropped rapidly in July and was never recovered above 1 µmole/g dry nodule/hr after August. There were considerable variations in the activity. The greatest variability occurred from July through October when the 95 percent confidence limits were over 90 percent of the mean. During the months of April, June, and July, the confidence limits were about 45 percent of the mean. The average annual acetylene reduction of 5- to 6-year-old varnishleaf shrubs was 6.2 µmole/g dry nodule/hr.

The seasonal pattern of acetylene reduction by 5- to 6-year-old deerbrush trees in Waters Creek site was similar to that of varnishleaf (Figure 7). The maximum rate was 14.8 µmole/g dry nodule/hr in June. The rates from August through October were also very low at this site. The variability of the rate was greatest in August when the 95 percent confidence limits were greater than 90 percent of the mean. The variability of the rate for deerbrush was

Figure 6. Seasonal pattern of acetylene reduction by 5- to 6-year-old varnishleaf at the Waters Creek site

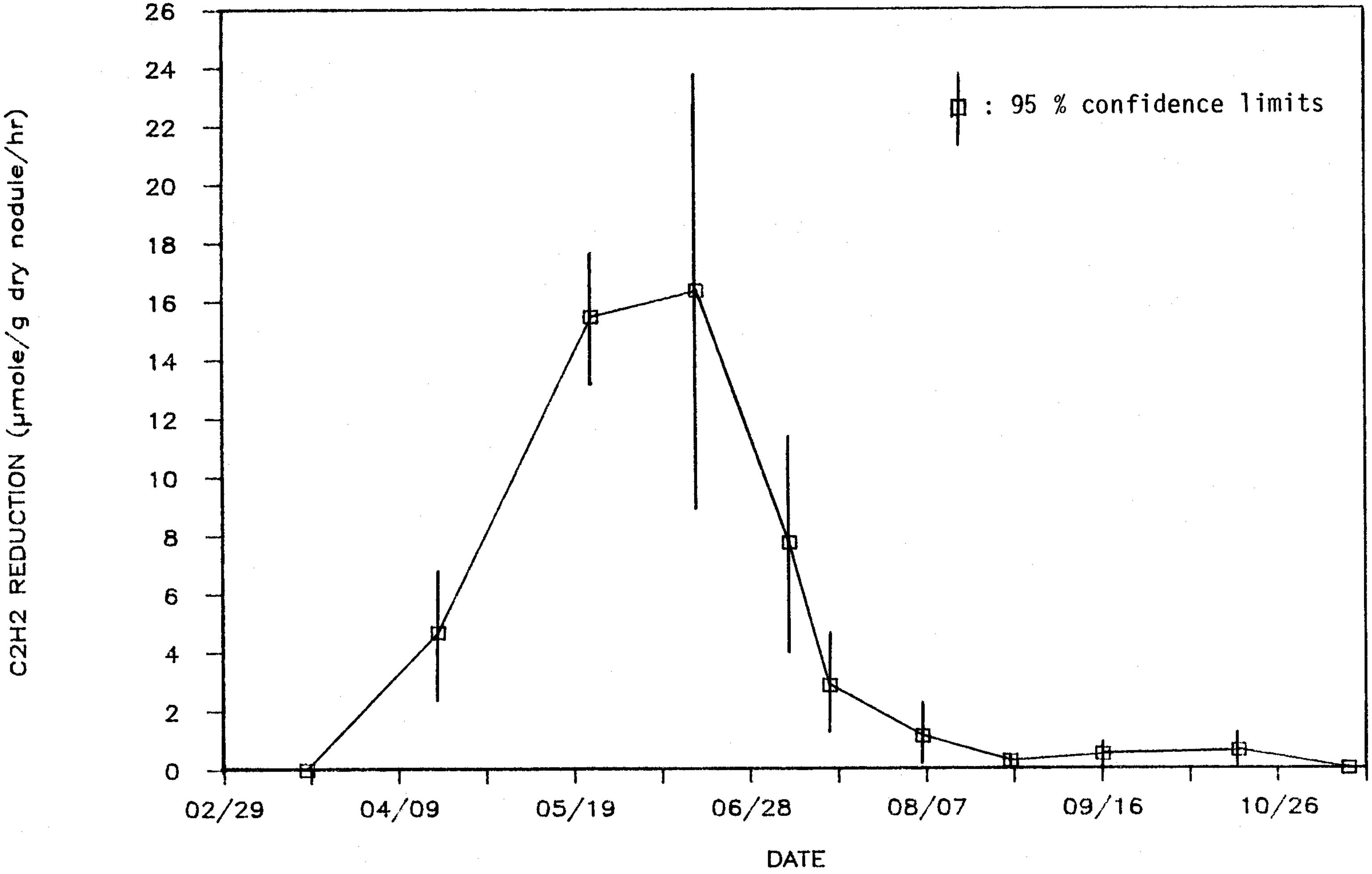
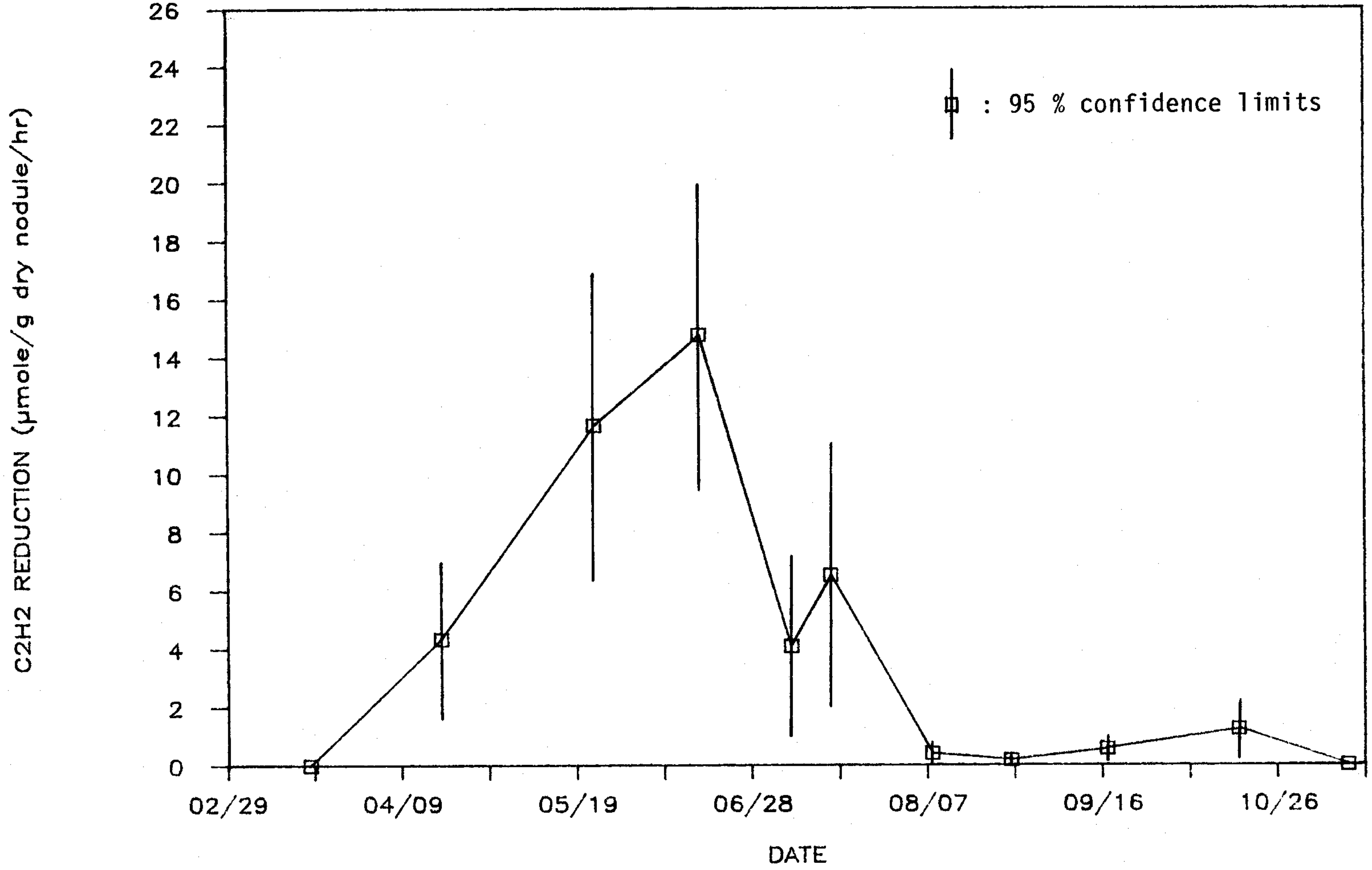


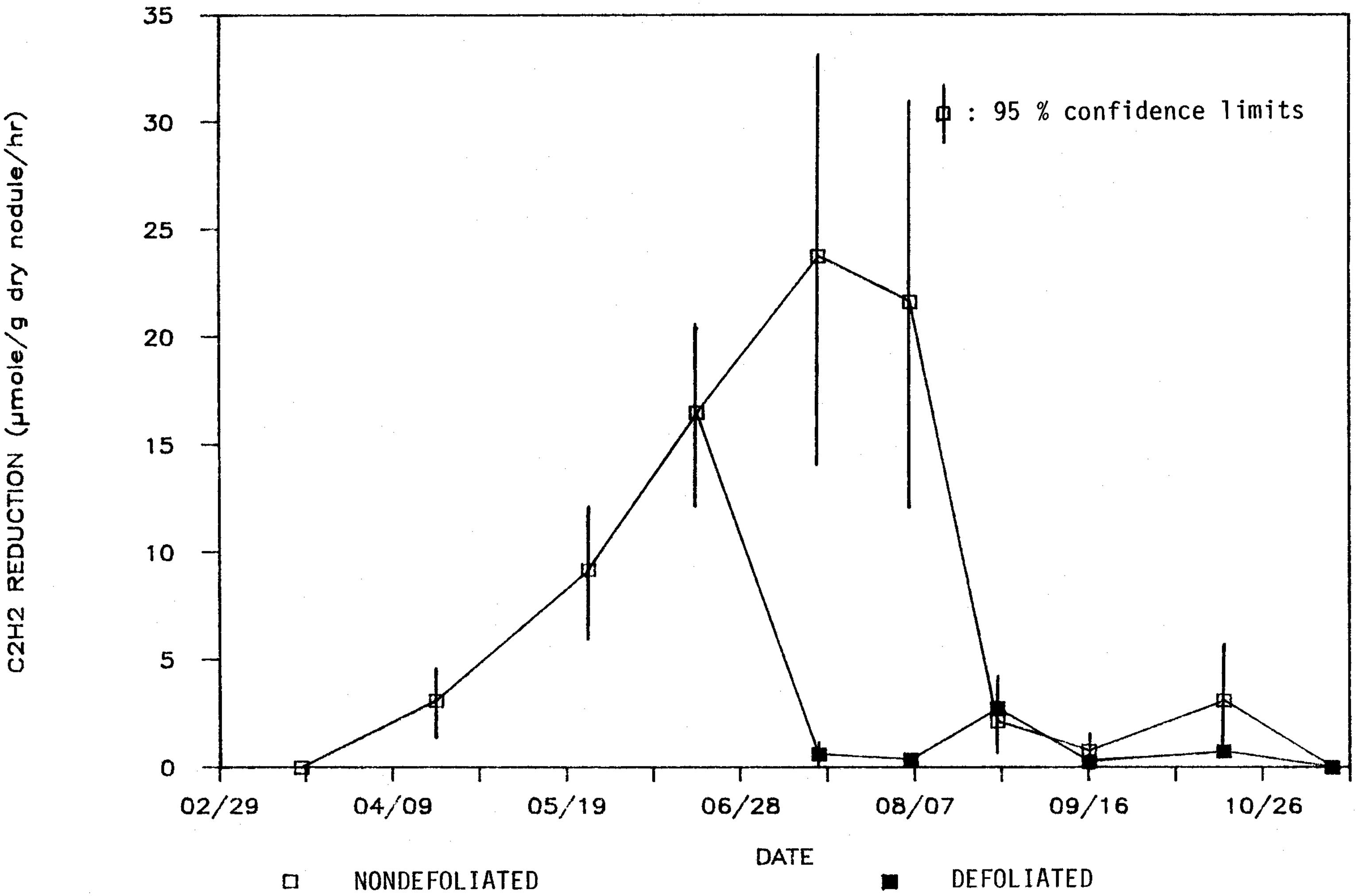
Figure 7. Seasonal pattern of acetylene reduction by 5- to 6-year-old deerbrush at the Waters Creek site



generally higher than that for varnishleaf except in June, when the confidence limits of deerbrush were about 40 percent of the mean. The average annual acetylene reduction of 5- to 6-year-old deerbrush shrubs was 5.5 μmole/g dry nodule/hr.

The seasonal pattern of acetylene reduction by 11-year-old snowbrush shrubs at the Windy Creek site was different from that for shrubs at the Waters Creek site (Figure 8). The maximum rate of 23.7 μmole/g dry nodule/hr occurred in July, and the rate was still high in early August (21.6 μmole/g dry nodule/hr). The rate dropped rapidly in late August but later recovered up to a rate of 3.1 μmole/g dry nodule/hr in October. At the site attacked by California tortoise-shell butterflies, the rate dropped to a minimal level with defoliation and did not recover significantly throughout the rest of the growing season. Considerable variability is also evident in Figure 8. When the activity was increasing and remained high, the 95 percent confidence limits were about 45 percent of the mean. When the rate was low at both attacked and unattacked sites, the confidence limits were 70 to 90 percent of the mean. The average annual acetylene reduction of 11-year-old snowbrush shrubs at the Windy Creek site was 9.8 μmole/g dry nodule/hr. However, the rate decreased to 4.6 μmole/g dry nodule/hr as a result of the attack by the California tortoise-shell butterfly.

Figure 8. Seasonal pattern of acetylene reduction by 11-year-old snowbrush at the Windy Creek site



Diurnal acetylene reduction

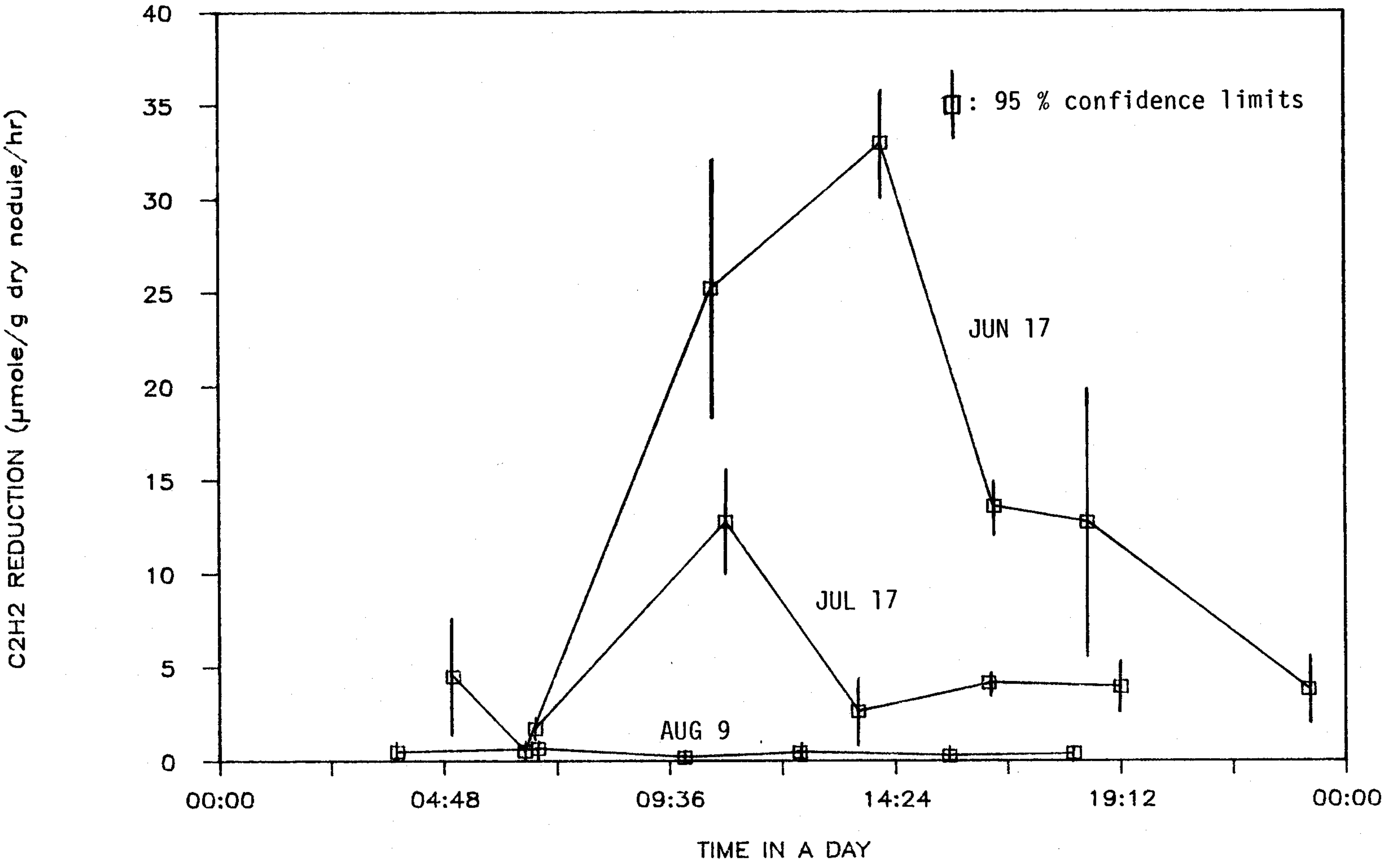
The diurnal pattern of acetylene reduction by deerbrush changed significantly during the months of June, July, and August (Figure 9). In June, when the monthly acetylene reduction was maximum for the year, the maximum rate of 33.0 μmole/g dry nodule/hr occurred at about midday. The maximum rate was six to seven times higher than rates occurring at night. In July, overall daily acetylene reduction rates dropped to less than one half of the rates during June. The maximum rate of 12.8 μmole/g dry nodule/hr occurred in the morning, and the rate dropped at midday. In August, acetylene reducing activity was very weak, and diurnal fluctuation was not evident. Mean acetylene reduction over 24 hours was calculated to be 14.8, 6.5, and 0.4 μmole/g dry nodule/hr for 17 June, 17 July, and 9 August, respectively.

Nodule biomass

There were two kinds of nodules at both study sites. Most of the nodules were small and scattered along the roots. On a few varnishleaf and snowbrush shrubs, nodules were found on a particular area where they grew in one large mass. In some cases, many small nodules were found in the area where woody litter was decaying.

Nodule biomass of 5- to 6-year-old varnishleaf and deerbrush was estimated by the equations given in Table 12. The average nodule biomass of 10 plots at the Warers Creek

Figure 9. Diurnal pattern of acetylene reduction by 5- to 6-year-old deerbrush at the Waters Creek site



site was 29.6 and 1.3 kg/ha for varnishleaf and deerbrush, respectively. The average nodule biomass determined from five snowbrush shrubs at the Windy Creek site was 155.6 kg/ha (Table 13).

Table 12. Linear regression of varnishleaf and deerbrush nodule biomass as a function of total aboveground biomass

Species	Equation*	Adjusted R^2	n
varnishleaf	$(\ln)Y = -7.740 + 1.264(\ln)X$	0.74	20
deerbrush	$(\ln)Y = -9.081 + 1.600(\ln)X$	0.95	15

* Y is nodule biomass and X is total aboveground biomass.

Nitrogen fixation

Annual nitrogen fixation estimated by the same method discussed in Chapter II was 8.29, 0.31, and 69.43 kg N/ha/yr for 5- to 6-year-old varnishleaf, deerbrush, and 11-

Table 13. Annual nitrogen fixation of <u>Ceanothus</u> species in southwestern Oregon

Species	Age	Density	Acetylene reduction*	Nodule biomass	Growth period	Nitrogen fixation
	yrs.	#/ha	µmole/g/ha	kg/ha	months	kg/ha/yr
CEVEL	5-6	24,222	6.24	29.64	7	8.29
CEIN	5-6	1,000	5.46	1.28	7	0.31
CEVEV**	11	3,360	9.76	155.61	7	69.43
CEVEV***	11	3,360	4.57	155.61	7	34.80

* Mean annual acetylene reduction.

** Normal snowbrush site. Stand density and nodule biomass are assumed to be the same as those at the defoliated site.

*** Defoliated snowbrush site.

year-old snowbrush, respectively (Table 11). Annual nitrogen fixation of snowbrush was the highest of the *Ceanothus* species tested, which was due to the great amount of nodule biomass at the Windy Creek site. At the Windy Creek site attacked by the California tortoise-shell butterfly, annual nitrogen fixation decreased to 34.8 kg N/ha/yr.

Nutrient analysis

Nutrient concentrations in *Ceanothus* species in southwestern Oregon are shown in Table 14. Values represent the average of 6 samples. In general, nutrient concentrations in leaves and nodules were higher than those in stems and roots. Micronutrients such as Fe and Al were the exceptions. All *Ceanothus* species had high accumulations of Fe and Al in the nodules. Biomass estimates of *Ceanothus* species are shown in Table 15. Individual plants averaged 3.3, 3.4, and 9.5 stems per plant for varnishleaf, deerbrush, and snowbrush, respectively. The maximum number of stems per plant was 12, 6, and 22 for varnishleaf, deerbrush, and snowbrush, respectively. Nitrogen content was calculated from the biomass components and the nitrogen concentration in Table 12. At the Waters Creek site, 103.6 kg/ha of nitrogen was retained in varnishleaf, while 5.0 kg/ha of nitrogen was in deerbrush. In contrast at the Windy Creek site, 579.9 kg/ha of nitrogen was retained in snowbrush.

Table 14. Nutrient analysis of _Ceanothus_ species

		N	P	K	S	Ca	Mg	Mn	Fe	Cu	B	Zn	Al
		% dry weight						ppm dry weight					
CEVEL	Stem	0.60	0.04	0.53	0.03	0.54	0.07	77	39	2	11	6	21
	Root	0.86	0.05	0.46	0.04	0.86	0.09	73	166	4	22	13	431
	Leaf	1.37	0.10	0.85	0.06	0.90	0.16	128	86	3	14	8	76
	Nodule	1.53	0.08	0.95	0.07	1.17	0.36	51	593	14	23	17	1598
CEIN	Stem	0.65	0.05	0.32	0.03	0.41	0.09	82	76	3	12	6	21
	Root	0.67	0.05	0.33	0.03	0.33	0.07	64	169	4	10	8	414
	Leaf	2.09	0.11	0.94	0.09	1.52	0.28	204	203	5	30	15	282
	Nodule	2.80	0.11	0.66	0.08	0.60	0.30	92	528	10	32	23	1639
CEVEV	Stem	0.77	0.11	0.54	0.05	0.67	0.05	63	73	3	14	6	63
	Root	0.68	0.09	0.41	0.06	0.99	0.06	68	257	4	11	18	389
	Leaf	2.02	0.21	0.79	0.09	0.73	0.11	110	232	4	22	13	256
	Nodule	2.10	0.11	0.74	0.08	0.94	0.20	106	1119	8	21	18	2090

* CEVEL = varnishleaf
CEIN = deerbrush
CEVEV = snowbrush

Table 15. Stand density, biomass, and nitrogen content of *Ceanothus* study sites in southwestern Oregon

Location	Species		Mean	Nitrogen content (kg/ha)
Waters Creek	CEVEL	No. of plants (#/ha)	24,222	
		No. of stems (#/ha)	80,111	
		Stem biomass (kg/ha)	7,813	46.9
		Root biomass (kg/ha)*	3,175	27.3
		Leaf biomass (kg/ha)	2,110	28.9
		Nodule biomass(kg/ha)	30	0.5
		Total	13,128	103.6
	CEIN	No. of plants (#/ha)	1,000	
		No. of stems (#/ha)	3,444	
		Stem biomass (kg/ha)	393	2.6
		Root biomass (kg/ha)*	147	1.0
		Leaf biomass (kg/ha)	66	1.4
		Nodule biomass(kg/ha)	1	0.0
		Total	607	5.0
Windy Creek	CEVEV	No. of plants (#/ha)	3,360	
		No. of stems (#/ha)	32,000	
		Stem biomass (kg/ha)	45,622	351.3
		Root biomass (kg/ha)*	16,402	111.5
		Leaf biomass (kg/ha)	5,633	113.8
		Nodule biomass(kg/ha)	156	3.3
		Total	67,945	579.9

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* Root biomass was calculated using a root:shoot ratio of 0.32 for *C. greggii* (Miller and Ng, 1977).

DISCUSSION

At the Waters Creek site, seasonal patterns of acetylene reduction by varnishleaf and deerbrush were similar to each other. Both species showed very low acetylene reduction rates from August through October, which probably is due to summer drought evident in Figures 10 and 11. Precipitation averaged over a 20-year period in southwestern Oregon was at a minimum in July, and soil moisture content was at a minimum in August. The acetylene reduction rates did not recover in the fall, which differed from the seasonal pattern of acetylene reduction for red alder in Washington (Tripp _et al._, 1979) and snowbrush in the western Oregon Cascades (Cromack _et al._, 1979).
In May, the acetylene reduction rate was higher by 2 to 5 μmole/g dry nodule/hr at the Waters Creek site than at the Windy Creek site. When the moisture is not a limiting factor, acetylene reduction rate seems to be affected by temperature. Acetylene reduction rates for both species at the Waters Creek site dropped in July in spite of the optimum soil temperature of 23.9 ^{o}C (Figure 12). Wollum and Youngberg (1969) found that 23-26 ^{o}C temperatures were optimum for snowbrush nodule formation and growth under greenhouse conditions. In this study, however, nitrogenase activity was suppressed by the severe moisture stress in July. Dalton and Zobel (1977) found that acetylene reduction rates of _Purshia tridentata_ were affected by moisture stress.

Figure 10. Typical pattern of precipitation distribution in five southwest Oregon counties

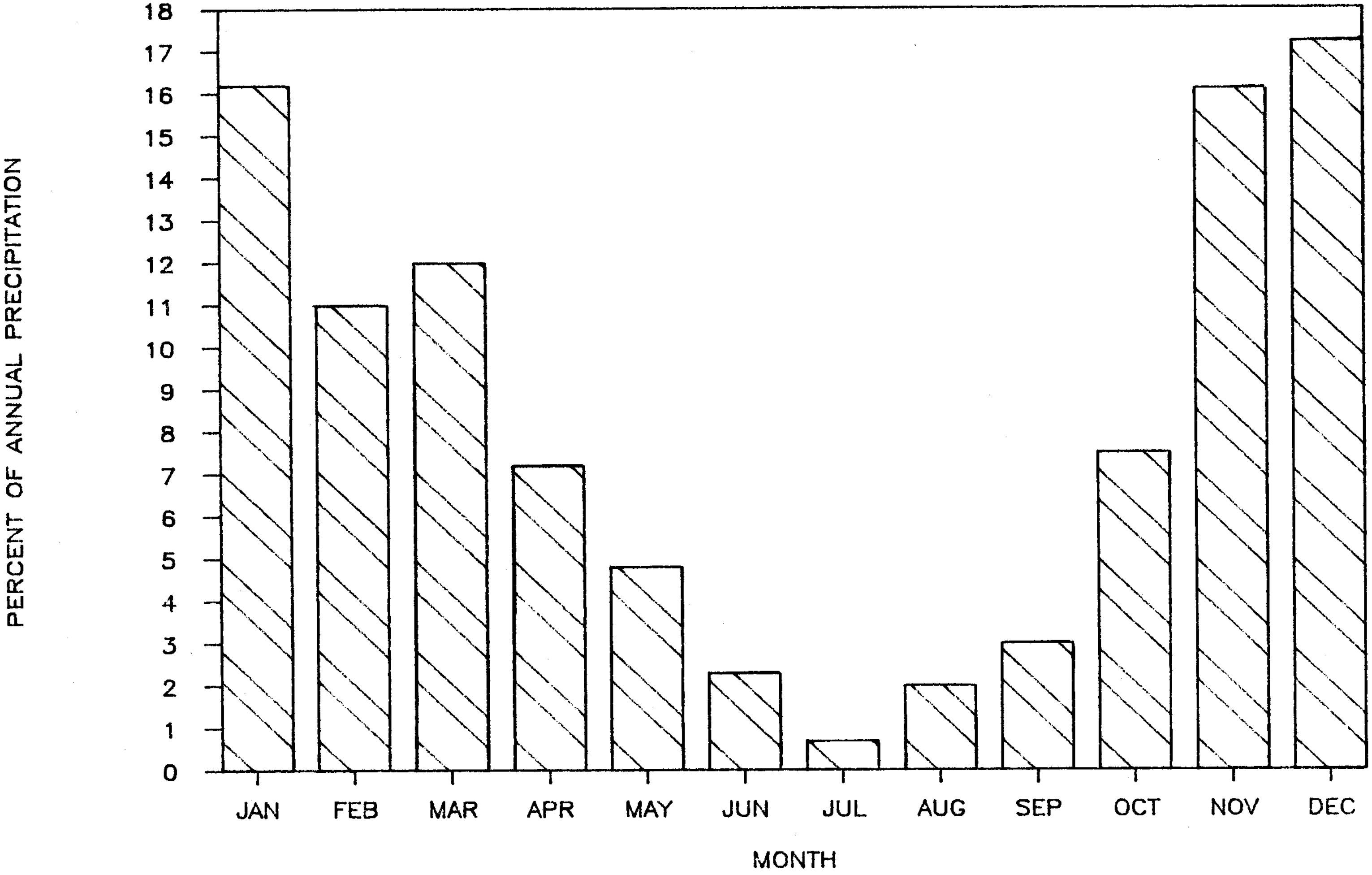


Figure 11. Soil moisture content at *Ceanothus* sites

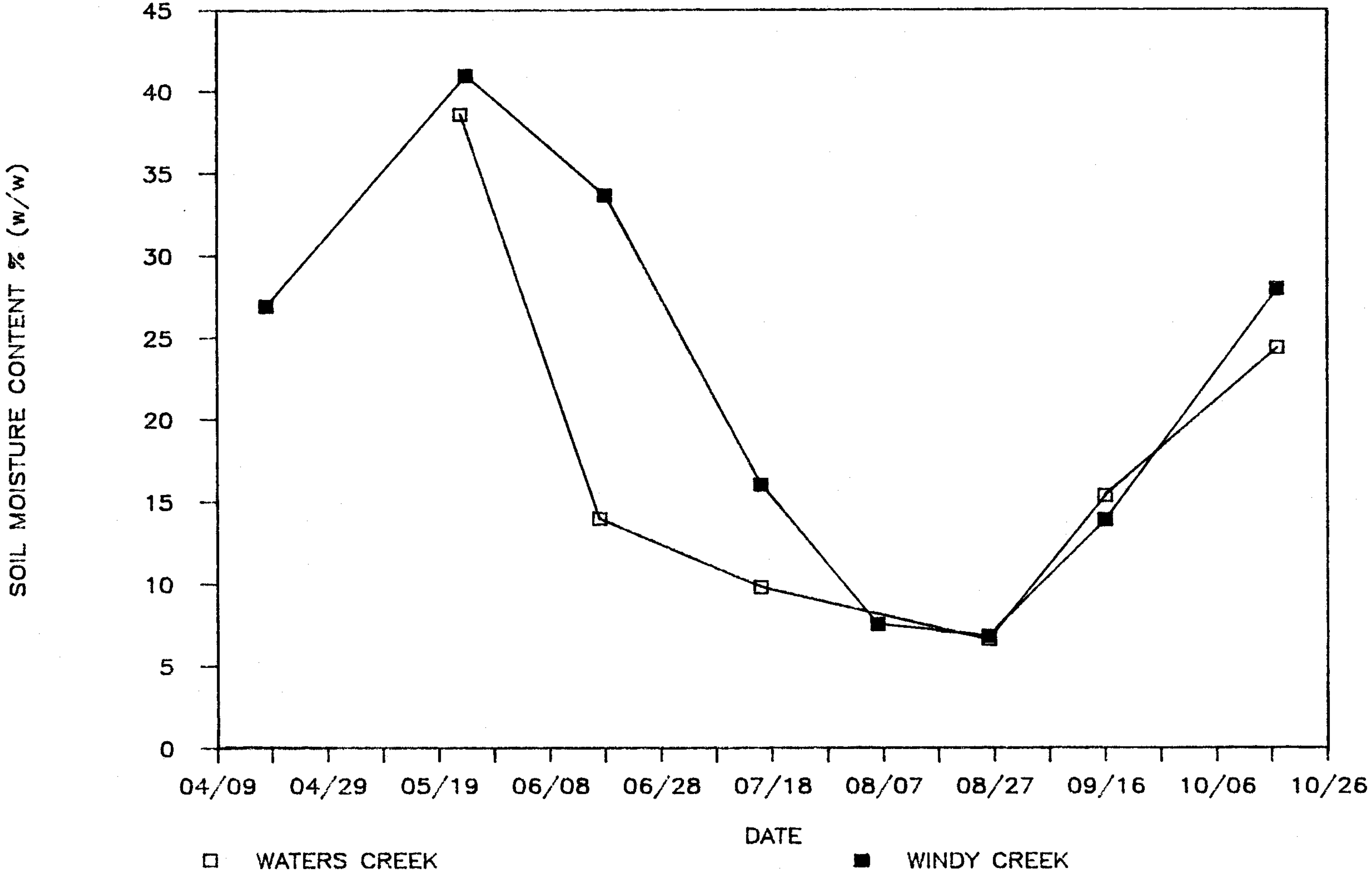
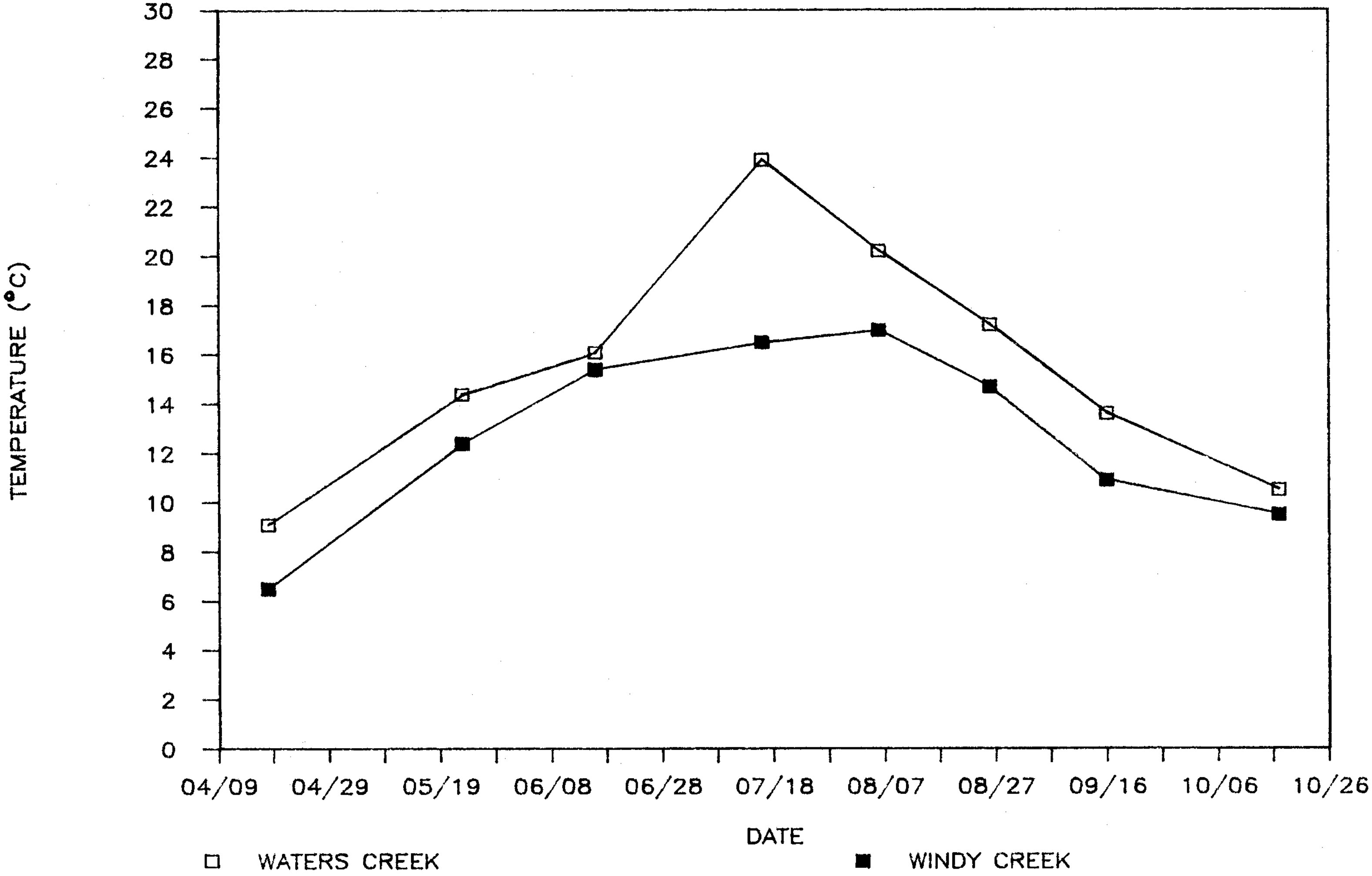


Figure 12. Soil temperature at *Ceanothus* sites (30 cm depth)



It seems probable that the diurnal pattern of acetylene reduction by deerbrush was affected by moisture stress. In July, diurnal shut down of acetylene reduction occurred at midday. In August, the rates were at a minimum level throughout the day when there was severe moisture stress.

Acetylene reduction rates ranged from 0.2 to 16.4 μmole/g dry nodule/hr for varnishleaf and from 0.2 to 14.8 μmole/g dry nodule/hr for deerbrush. Maximum rates for both species were about three times higher than the rates measured in the western Oregon Cascades (McNabb and Cromack, 1983). The variability of acetylene reduction rates for _Ceanothus_ species was greater than those for red alder (Tripp _et al_., 1979). More samples appear to be needed in order to obtain reasonable estimates of acetylene reduction for _Ceanothus_ species.

The maximum acetylene reduction rate for 11-year-old snowbrush at the Windy Creek site occurred one month later than the maximum rate at the Waters Creek site. At the Windy Creek site, the soil moisture content was higher than that at the Waters Creek site during the months of June and July (Figure 11). In southwestern Oregon, the relationship between potential evapotranspiration and elevation is statistically significant. During the dry season, potential evapotranspiration decreases less than 7.6 cm between 600 and 1500 m of elevation (Froehlich _et al_., 1982b). Soil nitrogen was higher at the Windy Creek site than at the Waters Creek site (Table 16). However, annual acetylene reduction activity at the Windy Creek site was higher than the activity at the Waters Creek site, which might have been caused by the lower moisture stress at the Windy Creek site. Acetylene reduction rates of varnishleaf and deerbrush were not much different from each other when they were growing at the same site. The difference between the rates of snowbrush and rates of other species could be explained by age and site differences. The maximum rate for 11-year-old snowbrush was about four times higher than the rate for 17-year-old snowbrush in the western Oregon Cascades (McNabb and Cromack, 1983). The 69.4 kg N/ha fixed by the 11-year-old snowbrush in this study represents 69 percent of the 101 kg N/ha fixed by the 17-year-old snowbrush reported by McNabb and Cromack (1983).

Table 16. Soil N and C at *Ceanothus* sites*

	Soil N $\bar{X} \pm SE$	Soil C $\bar{X} \pm SE$	C/N ratio $\bar{X} \pm SE$
	ppm		
Waters Creek	572 ± 81	14,750 ± 2,088	26 ± 4
Windy Creek	983 ± 101	32,420 ± 3,337	33 ± 3

* Sampled upper 30 cm of soil (n = 6).

The unpredictable mass movement of California tortoise-shell butterfly caused a considerable loss in nitrogenase activity of snowbrush at the Windy Creek site. Feeding on *Ceanothus*, high populations of the caterpillars virtually defoliated the plants. It was concluded by Wheeler (1971) that a substantial part of the nodular carbohydrate in red alder was unavailable for the purpose of nitrogen fixation, and maximal rates of fixation are only attained when new photosynthates are entering the nodule in quantity. Assuming a similar requisite for photosynthate allocation in the Ceanothus species in this study, the lack of new photosynthates in the snowbrush nodules may explain the rate decrease following the defoliation. Annual nitrogen fixation at the defoliated site was reduced to about one half that at the normal site.

Nodule biomass of 5- to 6-year-old varnishleaf at the Waters Creek site (29.6 kg/ha) was very low compared to that of other nodulated plants (Table 8) and that of 11-year-old snowbrush at the Windy Creek site (155.6 kg/ha). An 11-year-old snowbrush stand in northeast Oregon had a nodule biomass of 146 kg/ha (D. H. McNabb, unpublished data). Nodule biomass of a 17-year-old snowbrush stand in the western Oregon Cascades was 750 kg/ha (McNabb and Cromack, 1983). Nodule biomass of 5- to 6-year-old deerbrush at the Waters Creek site was the lowest (1.3 kg/ha) because of the low density of deerbrush at the site.

The estimates of annual nitrogen fixation by Ceanothus species are listed in Table 17. Nitrogen fixation of the 5- to 6-year-old varnishleaf stand was less than the averages obtained by other researchers. The low nitrogen fixation of varnishleaf was caused by low nodule biomass, which was probably due to the immaturity of the plants. A snowbrush stand showed an annual accretion rate of 108 kg/ha for the first 10 years, then the accretion rate decreased to 40 kg/ha during the period from years 10 through 15 (Youngberg *et al*., 1979). McNabb and Cromack (1983) found that a 17-year-old snowbrush stand was slightly overmature. Total nitrogen fixation of 8.6 kg/ha/yr in a 5- to 6-year-old *Ceanothus* stand at the Waters Creek site is the lowest of the *Ceanothus* studies in Table 17. Mean annual acetylene reduction of 11-year-old snowbrush was about two times higher than the rate of 5- to 6-year-old varnishleaf (Table 13). However, annual nitrogen fixation was estimated at about eight times higher in the snowbrush stand (69.4 kg/ha/yr) than in the varnishleaf stand (8.3 kg/ha/yr), which was due to the large difference in nodule biomass. Annual nitrogen fixation of 11-year-old snowbrush at the Windy Creek site was about the average of other results in Table 17.

The density of the 5- to 6-year-old varnishleaf stand was well above that of 11-year-old snowbrush at the Windy Creek site and greater than that of a 17-year-old snowbrush stand found by McNabb and Cromack (1983). The number of stems per plant in the varnishleaf was lower than the number in 17-year-old snowbrush plants. Stand biomass and total nitrogen in the varnishleaf stand was below those of other older snowbrush stands. The density of the 11-year-old snowbrush stand was less than that of a 17-year-old

Table 17. Estimates of annual nitrogen fixation by *Ceanothus* species

Annual N fixation (kg/ha/yr)	Location	Age (yrs)	Component	Reference
Ceanothus sp.				
60	Northern California	-	Ecosystem[a]	Delwiche et al. 1965
Ceanothus integerrimus				
0.3	Southwestern Oregon	5-6	Ecosystem[c] (1,000/ha)	This study
Ceanothus sanguineus				
24-50	British Columbia	0-10	Soil 0-15cm[b]	Binkley and Husted 1983
24-50	British Columbia	0-12	Ecosystem[b]	"
Ceanothus velutinus var. *laevigatus*				
8.3	Southwestern Oregon	5-6	Ecosystem[c] (24,222/ha)	This study
Ceanothus velutinus var. *velutinus*				
108	Oregon, western Cascades	0-10	Ecosystem[b]	Youngberg and Wollum 1976
70	Oregon, western Cascades	0-10	Ecosystem[b]	"
40	-	10-15	Ecosystem[b]	Youngberg *et al*. 1979
80	Oregon, western Cascades	17	Ecosystem[c]	Cromack *et al*. 1979
32	Northwestern Oregon	11	Ecosystem[c]	McNabb *et al*. 1979

Table 17. (continued)

Annual N fixation (kg/ha/yr)	Location	Age (yrs)	Component	Reference
42-48	Oregon, central Cascades	0-12	Ecosystem[d]	Binkley *et al.* 1982
94-100	Oregon, central Cascades	0-12	Ecosystem[d]	"
0-20	Oregon Cascades	0-15	Ecosystem[d]	Zavitkovski and Newton 1968
101	Oregon, western Cascades	17	Ecosystem[c]	McNabb and Cromack 1983
69	Southwestern Oregon	11	Ecosystem[c] (3,360/ha)	This study
35	Southwestern Oregon	11	Ecosystem[c]	This study (attacked by butterfly)

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[a] Based on atmospheric N^{15} method.
[b] Based on accretion studies.
[c] Based on acetylene reduction assays.
[d] Based on chronosequence method.

snowbrush stand found by McNabb and Cromack (1983). For 11-year-old snowbrush, the number of stems per plant was about three times higher than the number in 17-year-old snowbrush plants. Stand biomass and total nitrogen in 11-year-old snowbrush plants were near the median of those reported by Zavitkovski and Newton (1968).

When a *Ceanothus* stand is not mature, nitrogen supplied by *Ceanothus* is relatively low. Mature *Ceanothus* stands, however, supply substantial nitrogen to the ecosystem. Nitrogen supplied by *Ceanothus* is beneficial for crop tree growth. But pure and dense growth of *Ceanothus* may suppress the growth of conifer seedlings. *Ceanothus* density should be controlled to minimize the suppression of crop tree seedlings planted for regeneration. After overtopping *Ceanothus*, the crop trees will take advantage of nitrogen fixation by *Ceanothus*.

There is a question of whether *Ceanothus* can fix nitrogen as before when it is overtopped by crop trees. The behavior of *Ceanothus* under crop trees should be elucidated to understand the effect of *Ceanothus* on long-term site productivity. Better quantification and better understanding of the nitrogen fixation by *Ceanothus* will ensure more opportunities for *Ceanothus* to be used for forest management.

IV. SUMMARY AND CONCLUSION

1. Annual nitrogen fixation by 2-year-old red alder was 22.8 kg/ha/yr at the Alsea site and 17.5 kg/ha/yr at the OSU Field Laboratory. Annual nitrogen fixation by 58-year-old red alder was 50.1 kg/ha/yr at the Cascade Head Experimental Forest.
2. Nitrogenase specific activity by 2-year-old red alder ranged from 0.0024 to 85.1 μmole/g dry nodule/hr at the Alsea site and from 0 to 52.4 μmole/g dry nodule/hr at the OSU Field Laboratory. Nitrogenase specific activity by 58-year-old red alder ranged from 0.004 to 10.2 μmole/g dry nodule/hr. The activity of the old red alder was stable throughout a growing season.
3. Estimated nodule biomass was 121 kg/ha for the 58-year-old red alder at Cascade Head, and 16.3 kg/ha for 2-year-old red alder at the Alsea site, assuming a stand density of 10,000 trees/ha.
4. Red alder showed the potential for substantial nitrogen input into the ecosystem at 2 years and 58 years of age.
5. Annual nitrogen fixation by 5- to 6-year-old varnishleaf at the Waters Creek site was 8.3 kg/ha/yr. Annual nitrogen fixation by 5- to 6-year-old deerbrush at the Waters Creek site was 0.3 kg/ha/yr. The low nitrogen fixation was due to the low nodule biomass. Annual nitrogen fixation by 11-year-old snowbrush was 69.4 kg/ha/yr.

6. Following the attack of California tortoise-shell butterfly, and the subsequent defoliation, annual nitrogen fixation by snowbrush decreased to 34.8 kg/ha/yr.
7. The seasonal patterns of nitrogen fixation by 5- to 6-year-old varnishleaf and deerbrush growing at the Waters Creek site were similar to each other. The seasonal pattern of nitrogen fixation by 11-year-old snowbrush at the Windy Creek site was different from that of the other *Ceanothus* species at the Waters Creek site.
8. Estimated nodule biomass was 155.6 kg/ha for 11-year-old snowbrush and 29.6 kg/ha for 5- to 6-year-old varnishleaf. Nodule biomass of 5- to 6-year-old deerbrush was 1.3 kg/ha, which was due to the low density of deerbrush in the stand.
9. Nitrogenase specific activity seems to be predominantly affected by climatic conditions. Moisture stress was a major limiting factor for nitrogen fixation in this study.
10. At the Windy Creek site, 11-year-old snowbrush supplied a substantial amount of nitrogen to the ecosystem.

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