Water related characteristics
of some evergreen sclerophyll shrubs in central Chile

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ABSTRACT

Diurnal patterns of xylem water potential, the relations of leaf, osmotic, and turgor potentials to leaf relative water content, and the relations of leaf water vapor conductance to leaf relative water content were measured on four evergreen shrub species in central Chile and correlated with other plant activities. Depending on the species, maximum conductances were 0.13-0.33 cm.s^{-1}; minimum coudnctances occurred with relative water contents of 75-85% and leaf water potentials of — 35 to — 40 bars; osmotic potentials at full turgidity were — 25 to — 33 bars. Turgor was minimal with relative water contents of about 85%. Leaf conductances at given leaf water contents changed during the year, but the osmotic potentials at similar leaf water contents did not change measurably. The water relations of the Chilean shrubs were similar to those previously found for Californian shrubs. Shallow-rooted, evergreen shrubs compensate for rapid evaporational losses of water from the soil by having relatively high conductances when water is available and enduring low leaf water potentials when water is unavailable. Therefore, photosynthesis and growth rates of shallow-rooted shrubs vary more widely through the season than do rates of deep-rooted shrubs.

RÉSUMÉ

L'évolution diurne du potentiel hydrique du xylème, les relations entre le potentiel de la feuille, le potentiel osmotique, le potentiel de turgescence et la turgescence relative, ainsi que les relations entre la conductance de la feuille pour la vapeur d'eau et la turgescence relative ont été mesurées sur quatre espèces buissonnantes et corrélées à d'autres activités de la plante. Selon l'espèce les conductances maximales se sont situées entre 0,13-0,33 cm.s^{-1}; les conductances minimales ont correspondu à des turgescences relatives de 75-85 % et à des potentiels hydriques de la feuille de — 35 à — 40 bars; les potentiels osmotiques à la pleine turgescence ont été de — 25 à — 33 bars.

La turgescence était minimale pour une turgescence relative d'environ 85 %. Les conductances des feuilles correspondant à une teneur en eau déterminée ont varié dans le courant de l'année, tandis que les potentiels osmotiques correspondant à une teneur en eau donnée n'ont pas fait l'objet de variations mesurables. Le régime hydrique des buissons du Chili est semblable à ceux qui ont été mis en évidence précédemment chez les buissons de Californie.

Les buissons sempervirents à enracinement superficiel compensent les pertes rapides de l'eau du sol dues à l'évaporation par l'existence de conductances relativement élevées et par le fait qu'elles supportent des potentiels hydriques bas lorsque l'eau n'est pas disponible.

Pour cette raison, la photosynthèse et la croissance des buissons à enracinement superficiel subissent des variations saisonnières plus importantes que ce n'est le cas chez les buissons à enracinement profond.

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INTRODUCTION

Areas of the world with mediterranean-type climates have been intensively studied for several years to compare the structure and function of the vegetation and fauna (SPECHT 1969, DI CASTRI and MOONEY 1973, ECKARDT *et al.* 1977, MOONEY 1977, THROWER and BRADBURY 1977). Since the defining characteristics of the mediterranean-type climate are cool, wet winters and hot, dry summers, usually with limiting annual precipitation, plants growing in these areas can be expected to have both morphological and physiological adaptations to water stress (HARRISON *et al.* 1971, NG 1974, POOLE and MILLER 1975, MILLER 1978, MILLER *et al.* 1977, GILIBERTO and ESTAY 1978, NG and MILLER 1978). However, in spite of many studies concerned with the water balance of the vegetation and soil (BAUER 1936, MILLER 1947, SPECHT 1957 *a, b,* PILLSBURY *et al.* 1963, SHACHORI and MICHAELI 1965, SHACHORI *et al.* 1967, SPECHT and JONES 1971, SPECHT 1972), plant water relations have been little studied.

Previous studies in mediterranean regions showed species and geographic differences in plant water stress both diurnally and through the year (GRIFFIN 1973, SYVERTSEN 1974, POOLE and MILLER 1975, KRAUSE and KUMMEROW 1977, GILIBERTO and ESTAY 1978). These studies demonstrated distinct species segregation in the degree of water stress experienced by shrubs in California and Chile. For the major shrub species in the mediterranean region of California, POOLE and MILLER (1975) found the magnitudes of plant water stress and leaf conductances to be generally correlated with species rooting habit, as described by HELLMERS *et al.* (1955). The correlations imply morphological and physiological displacements which serve to minimize interspecific competition among the evergreen, sclerophyllous shrubs. The objective of this study was to measure some specific aspects of the water relations of four predominant evergreen, sclerophyllous shrub species in the mediterranean region of Chile and to relate these specific aspects to other species characteristics in order to clarify the adaptive strategies for limited water resources in mediterranean regions.

METHODS

Shrubs were measured at Fundo Santa Laura, 70 km NW of Santiago, Chile. MOONEY (1977) gives a general description of the research site. MILLER *et al.* (1977) describe the general microclimate of the north and south-facing slopes and ridgetop at the site. The four species studied were *Cryptocarya alba* (MOL.) LOOSER (Lauraceae), *Quillaja saponaria* MOL. (Rosaceae), *Lithraea caustica* (MOL.) H. ET ARN. (Anacardiaceae), and *Colliguaya odorifera* MOL. (Euphorbiaceae), which are common evergreen, sclerophyllous shrubs in the area (table). The shrubs are described more thoroughly in KUMMEROW and FISHBECK (1977). Nomenclature follows MUÑOZ (1959). The site was chosen because of its climatic and vegetational similarity to an intensively studied site in the mediterranean region of California (MOONEY 1977, THROWER and BRADBURY 1977). To document the climatic similarity, the macroclimate was measured from April 1972 through April 1977 using a pyrheliograph, a hygrothermograph in a standard weather screen, and a rain gauge.

Diurnal courses of xylem potentials were measured on stems from November 1974 through February 1975 on a south-facing (pole-facing) slope and on a ridgetop. Potentials were measured with a pressure chamber (WARING and CLEARY 1967) on three stems of each plant every 3 hours throughout the day, beginning before sunrise.

Internal leaf water relations were measured in February and March 1975 and November 1975 on stems that were cut from the shrub, recut under water, and left overnight in a saturated atmosphere. With this treatment, all samples which were cut from the stems and measured with the pressure chamber had xylem potentials above —3 bar and were assumed to be turgid. Total leaf water and osmotic potentials were measured using 1/4 inch (6735 mm) diameter leaf disks in Wescor C-15 thermocouple psychrometers, which were read with a Wescor MJ-55 microvoltmeter. The psychrometers were individually calibrated using various molar solutions of sodium chloride as described by LANGE (1967). All measurements were corrected for temperature using correction factors from WIEBE et al. (1971). Preliminary measurements were made with readings every 30 minutes to obtain equilibration times for each species. Generally, 4-6 hours were required for equilibration. The relations between leaf and osmotic potentials and leaf water content were obtained by removing leaves from a turgid stem, weighing them to obtain turgid weights, then allowing them to transpire under ambient conditions. Variable transpiring times gave a range of leaf water contents. The samples were then reweighed to obtain fresh weights. Leaf disks were removed to measure total leaf and osmotic potentials. Osmotic potentials were obtained by freezing the leaf disk in liquid nitrogen, then placing the disk in the sample holder. After the measurements, leaves and disks were oven-dried and weighed to obtain dry weights. Turgor potential was calculated by subtracting the osmotic potential from the total leaf water potential. Leaf water contents were expressed as relative water contents (RWC) which were calculated by:

(1) $$RWC = 100 \ (FW—DW)/(TW—DW)$$

where: TW is the leaf turgid weight, FW is the leaf fresh weight, and DW is the leaf dry weight.

The relation between leaf conductance and RWC was measured by weighing leaves repeatedly as they dried under light saturated conditions with moderate air movement, beginning with turgid leaves. Leaves were weighed every 5 minutes until the rate of water loss was constant, which usually required 2-3 hours. The rate of water loss was equated to a transpiration rate. The leaves were then oven-dried to obtain dry weights. During the weighing air temperature was measured with a thermocouple and vapor density was measured with a psychrometer. Leaf temperatures were measured with a thermocouple threaded into the leaf and were within 1°C of air temperatures. A combined leaf and air boundary layer conductance, h, was calculated as:

(2) $$h = W/[t \ (X_1—X_a) \ A]$$

where: W is the leaf weight loss during a time period, t is the length of the time period in seconds, X_1 is the saturation vapor density at leaf temperature, X_a is the vapor density of the air, and A is the leaf area.

In 1975 the turgid leaves were taken from the dark and weighing was begun immediately. Transpiration rates were initially low since stomates were closed in the dark; they increased as stomates opened in the light, then decreased as stomates closed because of water stress. These curves estimate water content at minimum conductance, but underestimate maximum conductance. In 1976 the turgid leaves were taken from the dark and

placed in the light in saturated air for 20-30 minutes. Thus, stomates could open in the light without transpiring before weighing began. These curves estimate maximum conductance and the decrease in conductance due to water stress. In 1973 leaf conductance on intact plants was measured through the day with a porometer described by KANEMASU *et al.* (1969). The highest of these values should underestimate the maximum conductance since some water stress was being experienced.
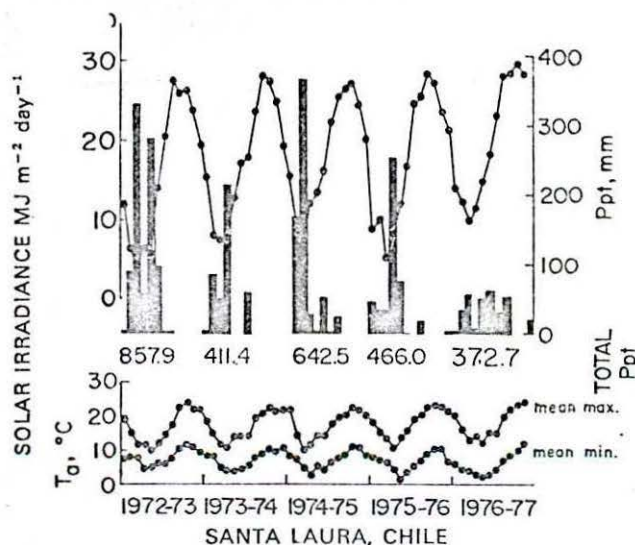

FIG. 1. — Solar irradiance ($MJ.m^{-2}.day^{-1}$), precipitation and air temperature from April, 1972, through March, 1977. Solar irradiance is given as monthly means, air temperature as monthly mean maximum and mean minimum, and precipitation as monthly totals.

RESULTS

Climatic conditions in Chile during the 5 years (*fig.* 1) were similar to those measured in California (POOLE and MILLER 1975, MILLER *et al.* 1977). At the Chilean site precipitation occurs mostly from May through September and averaged $550.10 \, mm.yr^{-1}$ during the 5 years. Solar irradiance varied from $6.3 \, MJ.m^{-2}.day^{-1}$ during the winter to $26.9 \, MJ.m^{-2}.day^{-1}$ in the summer. Air temperature was more moderate and less variable through the year in Chile than in California. From February 1973 to February 1974, 411 mm of precepitation were received. Air temperatures were 4-14°C in winter and 10-22°C in summer. Solar irradiance was about $8.0 \, MJ.m^{-2}.day^{-1}$ in winter and $27.3 \, MJ.m^{-2}.day^{-1}$ in summer.

Pre-dawn and midday xylem potentials showed species differences during the drought (*fig.* 2). In November 1974 the pre-dawn values of all species were —6 to —9 bar on the pole-facing slope and —5 to —10 bar on the ridgetop. By December, the pre-dawn values differed. The shallow rooted *Colliguaya* and *Cryptocarya* had potentials of —12 to —19 bar while the deep rooted *Quillaja* and *Lithraea* had

higher potentials of —4 to —14 bar. In early February 1975 the pre-dawn xylem potentials of the shallow-rooted shrubs were —16 to —36 bar and those of the deep-rooted shrubs were —8 to —19 bar. Some leaves of *Colliguaya* were yellow and beginning to fall, while those of *Lithraea* were still expanding. Shrubs on the ridgetop had lower potentials than shrubs on the pole-facing slope. *Colliguaya* and *Cryptocarya*
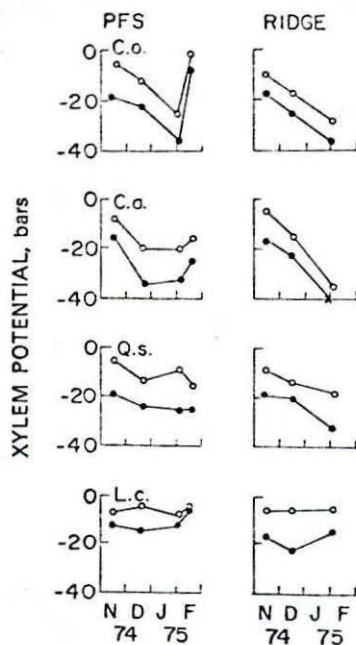

FIG. 2. — Pre-dawn (○) and midday xylem (●) water potentials of *Colliguaya odorifera* (C. o.), *Cryptocarya alba* (C. a.), *Quillaja saponaria* (Q. s.) and *Lithraea caustica* (L. c.) on the pole-facing slope (PFS) and ridge. Each point is the mean of three measurements. Readings marked X were below 40 bar.

developed the lowest water potential; *Lithraea* had the highest. By mid-February, following a rain, xylem potentials were higher (—2 to —16 bar). As pre-dawn potentials decreased, the difference between maximum and minimum potentials decreased in *Cryptocarya*, but remained constant with *Colliguaya* and *Quillaja*. Xylem potentials of *Lithraea* were always above —23 bars, while those of the other species were —30 to less than —40 bar. Leaf and osmotic potentials decreased as RWC decreased in all species but the relations differed (*fig.* 3). Leaf potentials decreased most rapidly with decreasing water content between 100 and 85 % (RWC) in *Colliguaya* (—3.7 bar/%) and least rapidly in *Quillaja* (—2.2 bar/%). Osmotic potentials of *Cryptocarya* and *Colliguaya* were below —30 bar at turgidity; those of *Quillaja* and *Lithraea* were about —25 bar. Between 100 and 95 % RWC osmotic potentials changed little in all species, although leaf water potentials changed

rapidly giving rapid decreases in the estimated turgidity. A line expressing the change in osmotic potential as water content decreases, assuming no change in solutes or cell colloids, passed through the data. A difference in the relations between the component potentials and RWC in February and November 1975 could not be detected from the ±4 bar variation in the measurements. A change, if one occured, was less than 3 bar.
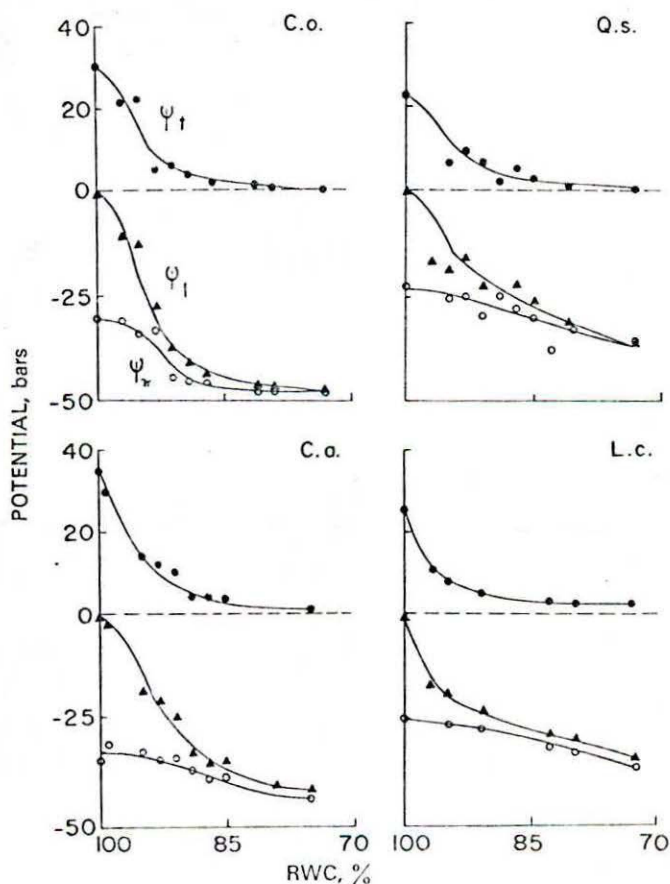

FIG. 3. — Relations of leaf (▲), osmotic (○), and turgor (●) potentials to relative water content (RWC). Species designations are the same as in Figure 2. Each point is the mean of 3-5 measurements.

Leaf conductance relations differed by species (*fig. 4*). Maximum conductances were 0.13-0.33 cm.s^{-1} (table). *Colliguaya* had the highest conductance and *Lithraea*, the lowest. Conductances were lower in February, after the summer drought, than in November. Conductances in *Colliguaya* were highest on the upper surface (0.17 and 0.05 cm.s^{-1}, top and bottom respectively), those of *Quillaja*

about equal on both surfaces (0.13 and 0.11 cm.s^{-1}) and thoses of *Cryptocarya* and *Lithraea* were highest on the lower surface (0.007 and 0.12 cm.s^{-1} for *Cryptocarya* and 0.002 and 0.12 cm.s^{-1} for *Lithraea*). Conductances were minimal (0.02-0.07 cm.s^{-1}) at leaf water contents of 50-93 %. *Cryptocarya* had the
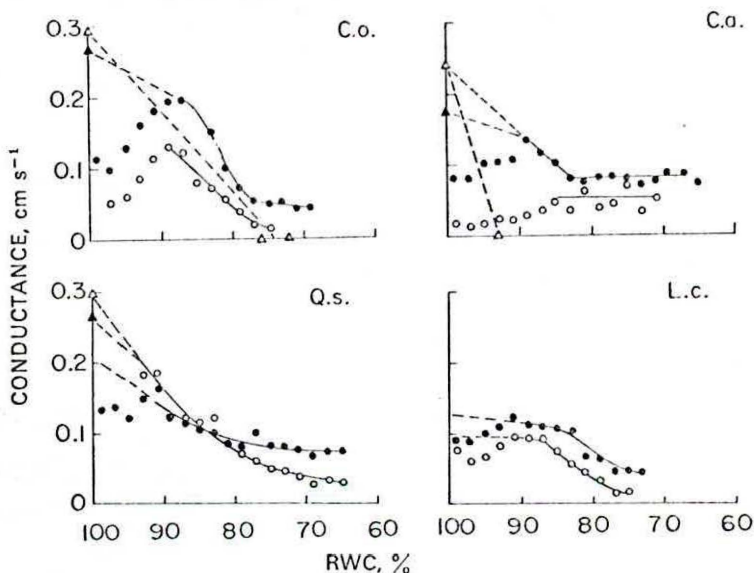

FIG. 4. — Relation of leaf conductance to leaf relative water content. Designations are the same as in Figure 2. Each point is the mean of 8-10 measurements. Dashed lines are extrapolations. ▲, January, 1973; ○, March, 1975; ●, November, 1975; △, December, 1976.

highest water contents at minimum conductances, *Quillaja* the lowest. The water contents and potentials at which conductances were minimal were similar in February 1975, November 1975 and December, 1976. The leaf water potential at which conductances were minimal were lowest in *Colliguaya* (—46 bar) and highest in *Lithraea* (—35 bar).

DISCUSSION

Although all species studied showed the same general pattern for water potential and leaf conductance as water deficits developed, the magnitudes and rates of change differed by species. These differences correlated with other plant characteristics. *Colliguaya* and *Cryptocarya*, which have the shallowest root systems (RIVEROS et al. 1976, GILBERTO and ESTAY 1978), had lower osmotic potentials and higher leaf conductances than *Lithraea* and *Quillaja*, which have been found to have large, deep roots (RIVEROS et al. 1976, GILBERTO and ESTAY 1978).

We postulate that the differences in the rooting patterns of the coexisting species reduce the competition for water, and lead to other correlated characteristics.

Shallow-rooted plants, in order to use water before it is lost by soil evaporation, have high leaf conductances to use soil moisture rapidly while it is available and low osmotic potentials to absorb water rapidly and to prolong the period during which soil moisture can be absorbed. These plants endure low water potentials but maintain reasonable tissue water contents. Deep-rooted plants can have lower maximum conductances and higher osmotic potentials since soil moisture is lost at a slower rate. Since photosynthesis is related to leaf conductances and growth is related to turgor potential, photosynthesis and growth should vary more widely through the year in more shallow-rooted plants than in deep rooted plants. The postulated differences in the seasonality of growth are supported in Chile by KUMMEROW and FISHBECK (1977) who showed that leaf initiation in *Colliguaya* occurs only during the wet months of the year, while that of *Lithraea* occurs throughout most of the year. The postulated differences in photosynthesis are supported by ROBERTS and MILLER (1977) who showed that the interception of solar irradiance was more variable seasonally in *Colliguaya* than in *Lithraea* and by Oechel (unpubl.) who measured maximum net photosynthetic rates 5-6 times greater in *Colliguaya* than in *Lithraea*, while values for *Quillaja* and *Cryptocarya* were intermediate and similar to each other.

The water relations and seasonality patterns of the Chilean shrubs are similar to shrubs in the mediterranean region of California. The diurnal courses of xylem potentials of the Chilean shrubs were segregated by species similarly to Californian shrubs measured by POOLE and MILLER (1975), particularly when analogous pairs of species (KUMMEROW and FISHBECK 1977) are compared. *Lithraea* in Chile and *Rhus ovata* in California are similar in appearance with, broad, hypostomatous leaves and deep extensive root systems (KUMMEROW and FISHBECK 1977). Both species have relatively low maximum leaf conductances (0.15 and 0.26 cm.s^{-1}, respectively), high xylem potentials when leaf conductances are minimal (-16 and -25 bar), and comparatively high xylem potentials throughout the summer drought. *Colliguaya* in Chile and *Arctostaphylos glauca* in California have steeply inclined amphistomatous leaves about 1 cm in diameter, a shallow-rooting habit (HELLMERS *et al.* 1955, MILLER and NG 1977, KUMMEROW *et al.* 1977, HOFFMANN *et al.* 1978). These have relatively high leaf conductances (0.32 and 0.50 cm.s^{-1}, respectively), and reach the lowest xylem potentials in each group of evergreen shrubs. *Quillaja* had moderate xylem potentials, as does *Quercus agrifolia* (GRIFFIN 1973).

These correlations of water relations, gross morphology, and seasonality of physiological activity imply species differences for utilizing water as a limiting resource and minimizing interspecific competition. Within the evergreen, sclerophyllous shrub root systems are stratified to reduce competition for soil moisture and constrain other physiological activities. Similar adaptations have been shown for other community types (GOODE 1956, MCWILLIAMS and KRAMER 1968). Shallow-rooted species should have higher leaf conductances, transpiration rates, photosynthetic rates and lower osmotic potentials while water is available, and greater

annual fluctuations in plant water potentials and growth than should deep-rooted species. Shrub species growing in mediterranean regions have adapted not only to survive the semiarid conditions but also to co-exist. Adaptations enabling co-existance may be morphological and physiological displacements which prevent the species from having the same activity patterns and directly competing for the same resource.

TABLE

Summary of leaf water characteristics. DW *is dry weight,* TW *is turgid weight,* RWC *is relative water content,* Ψ_l *is leaf water potential,* Ψ_π *is osmotic potential*

Species	Area/Leaf (cm²) a	DW/Area (g.m⁻²)		Water/Area (g.g⁻¹)		Water/TW (g.g⁻¹)	
		a	c	a	c	a	c
Colliguaya odorifera.	2.3 ± 0.2	170 ± 9	250 ± 23	266 ± 14	297	0.60 ± 0.01	0.54 ± 0.0
Quillaja saponaria...	6.0 ± 0.2	146 ± 9	208 ± 20	234 ± 7	277	0.61 ± 0.02	0.56 ± 0.0
Cryptocarya alba....	5.1 ± 0.4	146 ± 10	208 ± 20	232 ± 10	210	0.59 ± 0.03	0.53 ± 0.0
Lithraea caustica....	8.4 ± 0.4	–	164 ± 26	–	208	–	0.56 ± 0.0

Species	Maximum leaf conductance (cm.s⁻¹)				RWC at min. conductance (%)		Ψ_l at min. leaf conductance (bars)	Ψ_π at turgidity (bars)
	b	c	d	a	a	c-d		
Colliguaya odorifera.	0.27	0.26	0.33	0.30	75	72-76	— 46	— 31
Quillaja saponariaö..	0.27	0.26	0.18	0.30	50	64-68	— 40	— 24
Cryptocarya alba....	0.17	–	0.20	0.26	93	82-83	— 40	— 34
Lithraea caustica....	0.13	0.15	0.16	–	–	77-77	— 35	— 25

a, measured in December 1976; *b,* measured in January 1973 (n = 5); *c,* measured in February 1975; *d,* measured in November 1975.

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