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SEASONAL PATTERNS OF PLANT FLAMMABILITY AND MONOTERPENOID CONTENT IN *Juniperus ashei*

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Abstract—The susceptibility of *Juniperus* communities to prescribed fires can vary greatly throughout the year. The objective of this project was to determine the relationship between the seasonal concentration and composition of volatile oils and plant flammability in two Ashe juniper (*Juniperus ashei*) populations. Total monoterpenoid concentration was significantly affected by season and by plant population. Mean monoterpenoid concentration of a population from each central Texas was 9.16 mg/g fresh weight of juniper needles while the mean concentration of a west central Texas population was 11.62 mg/g of fresh weight. Monoterpenoid concentrations were typically lowest during the summer and highest during the spring and winter in the western population, but there was no seasonal pattern in the eastern population. The eastern population of trees was slightly (4.8%) more flammable than the western population, and male trees were slightly (3.8%) more flammable than female trees. The concentration of limonene was positively related to plant flammability and could increase flammability by 30% over the range of concentrations found in this species. Bornyl acetate was negatively related to flammability with each 1 mg/g increase in concentration resulting in a 2% decrease in flammability. Caloric energy content and percent leaf moisture were not significant factors in determining the percentage of the Ashe juniper plant actually burned. Secondary chemicals, usually considered as antiherbi-

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vore mechanisms, may also serve an important role in determining the likelihood of a plant being consumed by fire.

Key Words—Prescribed fire, volatile oils, juniper, monoterpenoids, flammability.

INTRODUCTION

The physiognomy of the Edwards Plateau region of Texas has changed from an open savanna with scattered trees to an almost closed woodland during the last 200 years (Smeins, 1980). Ashe juniper (*Juniperus ashei* Buchholz), a native tree of the Edwards Plateau, is not one of the dominant species in this area. This species may have been limited originally to rocky outcrops and steep canyons, but it has increased in density and range since the suppression of natural wildfires (Foster, 1917). Ashe juniper is vulnerable to fire-induced mortality when the tree is young (<2 m tall), but the susceptibility decreases with age (Bryant et al., 1983). As the plant matures, herbaceous production under the tree canopy decreases and consequently there is little fine fuel available for maintaining fire continuity (Fulhendorf et al., 1996).

Disturbances historically have been via either man-made or lightning-caused fires. Lightning-caused fires often originated during the hot, dry summer months whereas man-made fires (prescribed fires) are usually conducted in early to midwinter for increased safety. Besides the obvious differences in environmental conditions between summer and winter, plant flammability changes with season (Rodríguez Añón et al., 1995), potentially resulting in different fire intensities. Plant moisture (Wright and Bailey, 1982) and heat content of plant tissues (Rodríguez Añón et al., 1995; Philpot, 1969) vary seasonally and directly influence plant flammability. Plant phytochemicals, particularly monoterpenoids, may also increase the combustibility of plant material by increasing the probability of ignition (White, 1994).

Seasonal changes in monoterpenoids have been well documented for many coniferous species (Adams, 1987; Nerg et al., 1994; Riddle et al., 1996) but there does not appear to be a well-defined seasonal pattern in either the total concentration or the composition of individual monoterpenoids. Monoterpenoid concentrations were greatest in spring for Douglas fir [*Pseudotsuga menziesii* (Mirb). Franco] (Zou and Cates, 1995) and redberry juniper (*Juniperus pinchotii* Sudw.) (Riddle et al., 1996), but were greatest at the end of the growing season and lowest in the spring for western juniper [*Juniperus osteosperma* (Torr.) Little] and one-seeded juniper [*J. monosperma (Engelm.) Sarg.*] (Adams, 1987). These seasonal patterns may result from environmental variables such as soil moisture that vary seasonally and that may increase the concentration of some oils (e.g., α-pinene) while having no effect or even decreasing the concentration of other monoterpenoids (e.g., β-pinene, myrcene, limonene) (Gilmore, 1977). Other environmental factors such as soil fertility (Muzika et al., 1989; Mihaliak and Lincoln, 1985) and light (Klepzig et al., 1995) can also significantly affect the concentration and composition of monoterpenoids in plants.

To develop effective fire management systems for juniper communities, we need to understand the relationship between environmental factors, plant secondary chemicals, and flammability. The objectives of this study were to document the seasonal changes in secondary chemistry in Ashe juniper and to relate the observed changes in monoterpenoid concentrations and composition to plant flammability.

METHODS AND MATERIALS

Collection of Material. The study was conducted at the Sonora Research Station (31°N, 100°W) located 45 km southeast of Sonora, Texas, and on the Annandale Ranch (29°29′N; 99°44′W) near Concan, Texas. The two sites are approximately 120 km apart. Long-term average precipitation for both sites is approximately 60 cm/yr. Detailed site descriptions can be found in Riddle et al. (1996) and Owens (1996) for the Sonora and Annandale sites, respectively. Twenty Ashe juniper trees were permanently marked at each site in March 1993 and sampled approximately every six weeks for 16 months. At each site, 10 of the trees were male and 10 were female.

Approximately 80 g fresh weight of mature juniper foliage and twigs were collected at each sample date. Juvenile foliage was not collected because oil concentration is generally greater in mature foliage than in young foliage (Maarse and Kepner, 1970). Samples were collected from around the entire tree without regard to spatial location because spatial location within the canopy does not significantly affect monoterpenoid concentrations in leaf tissue (Hall and Langenheim, 1986). Twenty grams of sample were immediately placed in liquid nitrogen in the field and frozen for later analysis of oils and gross energy. Sixty grams were placed in a paper bag in a cooler for later analysis of flammability. Xylem water potential was measured at each sampling date to estimate water stress by using a pressure bomb (Scholander et al., 1965).

Chemical Extractions and Identification. Fifteen grams (fresh weight) of frozen juniper needles and small twigs were steam distilled in 150 ml water for 8 hr (Owens et al., 1998). The distillate was collected in 5 ml hexane, and tetradecane was added as an internal standard. After distillation, a 2-ml aliquot was withdrawn from the sample. Samples were stored at −80°C until lab analysis was complete. Analysis was performed on an HP 5890 gas chromatograph by using a methyl silicon capillary column (0.25 μm × 25 m) with a nitrogen carrier. The temperature program was 70°C for 2 min, a 1.5°C/min increase to

97°C, then a 6°C/min increase to 187°C, followed by a 15°C/min increase to 262°C with a 5-min plateau at 262°C. Injector temperature was 280°C, and the detector temperature was 240°C. Terpenes were identified by comparison with retention times of known external standards. Commercially available external standards were tricyclene, α-pinene, camphene, β-pinene, sabinene, myrcene, cymene, limonene, γ-terpinene, linalool, fenchyl alcohol, camphor, citronellol, borneol, terpinen-4-ol, terpineol, carvone, and bornyl acetate.

Energy Content and Flammability. Gross energy content was determined by using a bomb calorimeter with 1 g fresh weight of juniper needles. Wet weight, rather than dry weight, was used to determine the gross energy content of flammable tissue under seasonal conditions. Ten grams of fresh juniper needles were weighed, oven-dried at 60°C for 48 hr, and reweighed to determine gravimetric plant moisture.

Flammability was determined by placing 50 g of juniper needles and small twigs on a screen above an open flame. The open flame was placed under the sample for 60 sec and then removed. Four thermocouples were placed in the sample and one was placed between the sample and the open flame. Temperatures were recorded every 5 sec and averaged every min on a Campbell 21X data logger. After 5 min, the remaining sample was reweighed to determine the percentage of the plant material actually burned. If the sample was still burning at the end of the 5-min observation, it was extinguished and the remaining tissue was weighed.

Data Analysis. Seasonal changes in total concentration of the monoterpenoids and the concentration for each major compound were analyzed using split-plot models with site in the main plot and time in the split plot. The error term for the main plot was tree nested within site.

The relationship between plant flammability and plant characteristics was analyzed by using a growth curve model. Independent variables were the concentrations of the three dominant oils (camphor, bornyl acetate, and limonene), percent plant moisture, caloric content on a fresh weight basis and on a dry weight basis, site, tree sex, and xylem water potential. The dependent variable was the percentage of the plant that burned. Five different structures of the variance/covariance matrix were tested. The models were: (1) simple structure—where a single variance estimate was used over all time intervals and no correlation between time periods was assumed; (2) banded main diagonal—where the variance was allowed to vary with each sample date but there was still an assumption of no correlation between time periods; (3) compound symmetry—where a constant covariance between time periods was assumed but variance was allowed to vary by time period; (4) first-order autoregressive—where the variances were the same and the covariance was held constant between time periods, and (5) Toeplitz—where variances were the same and the covariances in one line up and down the diagonal were the same. This last model is similar to model 4 but allows a different rate of covariance in different time periods. The best model was selected using a likelihood ratio analysis with $\alpha = 0.05$.

RESULTS

Monoterpenoids. Total concentration of volatile oils was significantly greater ($P = 0.075$) in the Sonora population than in the trees at the Annandale Ranch (11.92 vs. 9.16 mg/g fresh weight, respectively). There was a strong seasonal effect ($P < 0.001$) on the volatile oil concentration at Sonora, where concentrations were greatest during the winter and spring months (January through May) and lowest during the summer and fall (Figure 1). There was no seasonal effect at the Annandale site, where monoterpenoid concentrations remained constant throughout the year.

Eighteen different monoterpenoids have been identified in Ashe juniper (Owens et al., 1998), but only 12 were present in sufficient quantity to analyze in this study. The remaining six were present in trace amounts and were not present in every month. The concentration of limonene, cymene, γ-terpinene, and myrcene were affected by the tree population ($P < 0.05$) with a greater concentration found in Sonora than in Annandale. The concentration of these four compounds was also affected by a significant interaction between the season

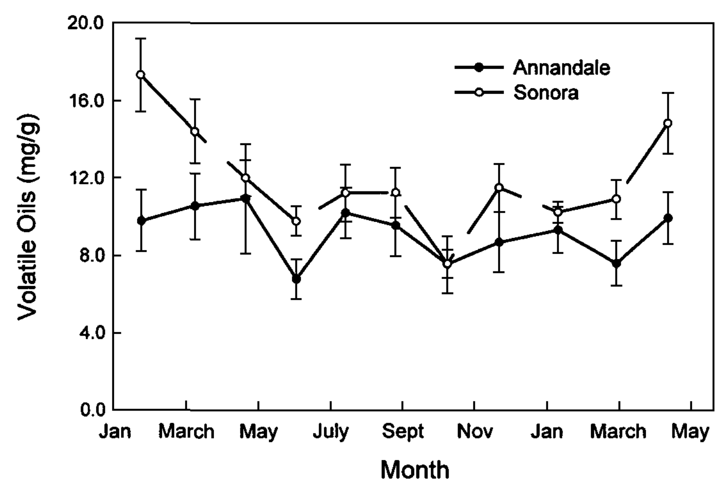

FIG. 1. Seasonal concentrations of monoterpenoids in Ashe juniper at two sites. Bars represent $\pm$ 1 SE.

of the year and the tree population (Figure 2, cymene not shown). An additional eight compounds (β-pinene, borneol, bornyl acetate, camphene, camphor, carvone, citronellol, and tricyclene) exhibited a seasonal change in concentrations that paralleled the changes observed for the total concentrations (Figure 2, only bornyl acetate shown). These monoterpenoids were not affected by the different populations of trees.

Plant Parameters. Percent moisture in the needles and fine twigs averaged about 44% on both sites throughout the year. There was a strong seasonal effect demonstrated by high plant moisture in winter and spring and low gravimetric plant moisture during the summer (Figure 3A). Gravimetric plant moisture ranged from 36 to 48% on the Annandale site and from 38 to 48% on the Sonora site.

Trees on the Sonora site exhibited significantly lower plant water potential ($\bar{X}$ = 2.1 mPa) than trees on the Annandale site ($\bar{X}$ = 1.7 mPa) throughout the year. On a seasonal basis, plant water potentials varied with low water stress during the winter months and increasing stress during the summer (Figure 3B). During the summer months of July and September, water potential dropped below the −3.5 mPa sensitivity of the pressure bomb. Xylem water potential was greater at the Sonora site than at the Annandale site during the second winter, which probably reflects the greater precipitation received in Sonora during the November to January time period (Figure 3C). Whenever precipitation at the Annandale site was greater than at the Sonora site (e.g., May, 1994), then xylem water potential at Annandale was also greater.

Mean caloric content of fresh needles and twigs was not significantly different between the two sites ($\bar{X}$ = 2.6 kcal/g fresh weight), although there was a significant interaction between the site and season. Energy content was least during the winter and spring months and greatest during the summer (Figure 3D). Energy content on a fresh weight basis was least at whichever site had the greatest precipitation.

Flammability. Plant flammability, as measured by the percentage of fresh needle and twig material burned, did not vary across the two research sites. Over the course of the year, an average of 78.8% of the fresh foliage burned, but there was a highly significant effect of the season of the year (Figure 4). During the peak spring growing period, only about 50% of the material burned, while almost 90% burned in the late growing season and the dormant winter period. During the summer, fire temperatures increased rapidly and reached almost 500°C within 2 min after the flame was placed under the sample (Figure 5A). The majority of the sample had burned after 3 min and temperatures dropped rapidly. Peak temperatures were over 500°C. Winter fires were less intense with peak temperatures reaching only 450°C after 3–4 min (Figure 5B).

The growth model analysis of plant flammability and plant characteristics was best described by the banded main diagonal model. Although all five models provided some degree of fit to the data, only the model allowing the variance

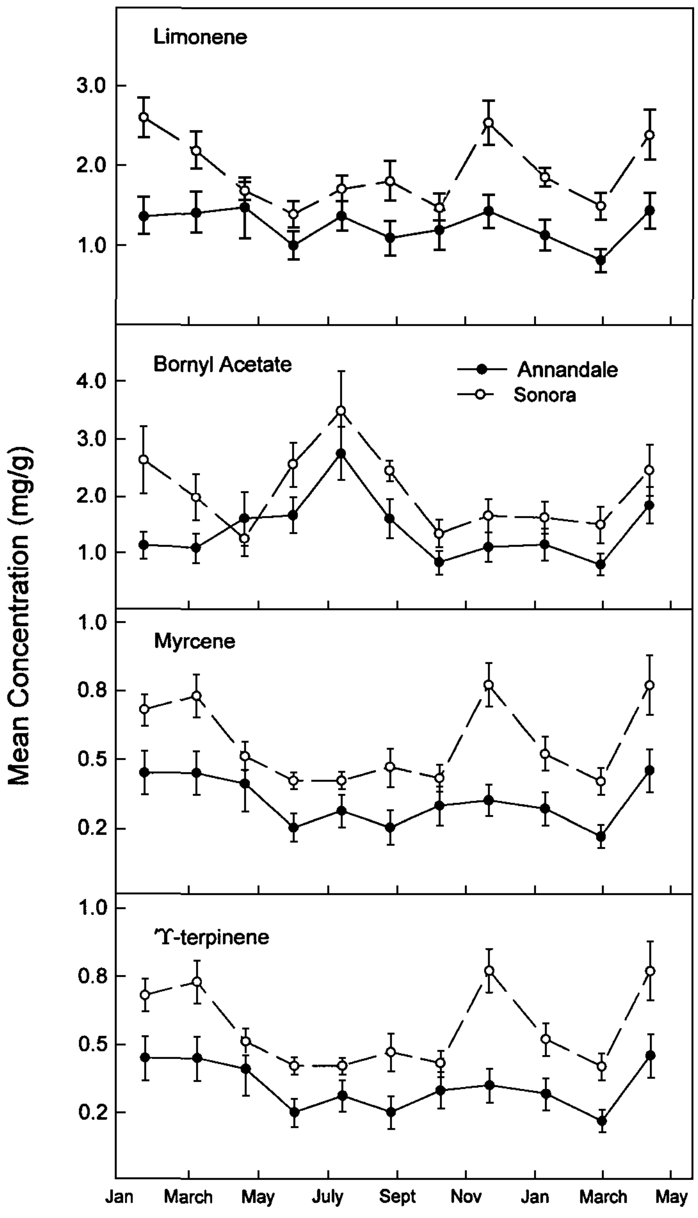

FIG. 2. Seasonal concentrations of limonene, bornyl acetate, myrcene, and γ-terpinene in Ashe juniper at two sites. Bars represent $\pm$ 1 SE.

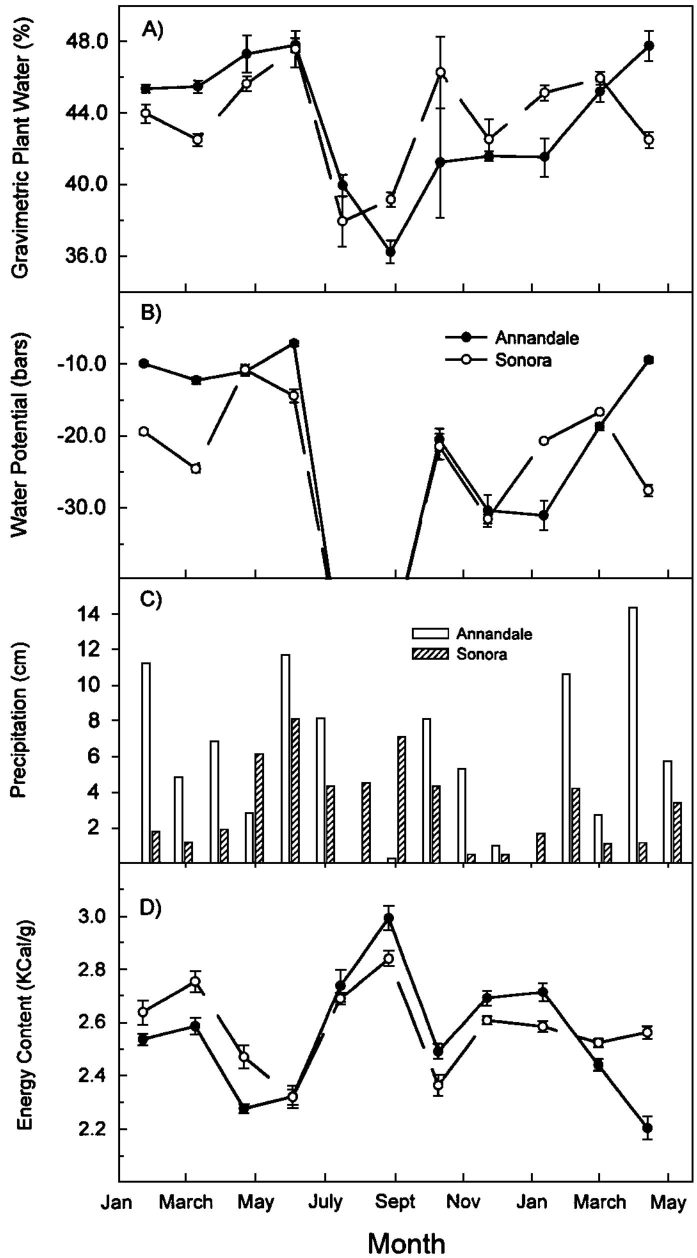

FIG. 3. Seasonal plant moisture characteristics and energy content for two populations of Ashe juniper and precipitation received at Annandale and Sonora sites over a 16-month period.

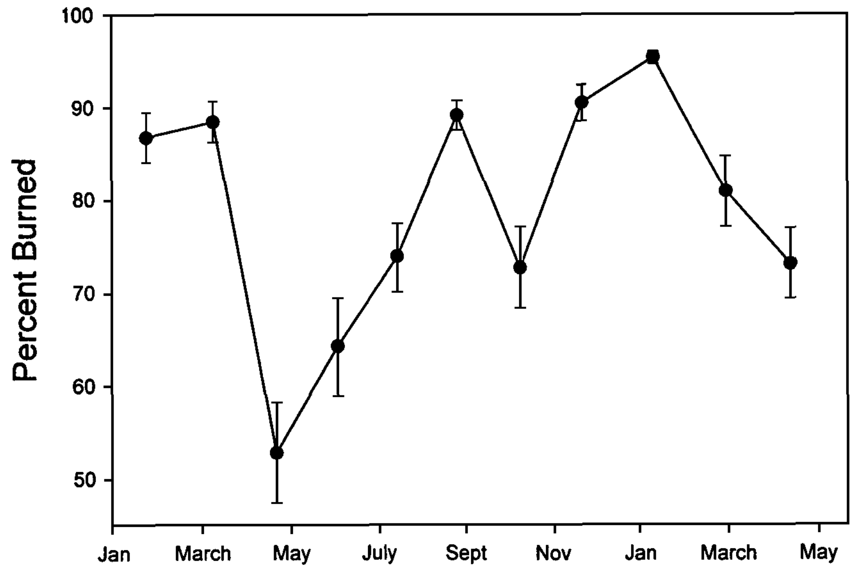

FIG. 4. Seasonal pattern of flammability of Ashe juniper. Bars represent ± 1 SE.

to vary across time periods and assuming no correlation between time periods (banded main diagonal) provided a better fit than the simple model that assumed a single variance across all time periods ($\chi^2 = 69.16$, $P \leq 0.001$). The compound symmetry ($\chi^2 = 1.73$, $P \leq 0.188$), first-order autoregressive ($\chi^2 = 1.83$, $P = 0.176$), and Toeplitz ($\chi^2 = 14.99$, $P = 0.132$) models were not significantly different than the simple model assuming a single variance. The plant population, sex of the tree, and the concentrations of bornyl acetate and limonene had a significant effect on the amount of the plant that burned (Table 1). Since the sex of the tree and the plant population were coded as binary variables, their net effect was to adjust the intercept of the model. Male trees were slightly (3.8%) more flammable than female trees, and trees from Annandale were slightly (4.8%) more flammable than trees at Sonora. The concentration of limonene has a gross positive effect on flammability, whereas the concentration of bornyl acetate had a gross negative effect. Over the concentrations of these two compounds actually found in the plants, limonene could increase flammability by nearly 30% while bornyl acetate decreased flammability by about 10%

DISCUSSION

Ashe juniper trees at Sonora contained about 30% more monoterpenoids than trees at the Annandale Ranch. This is in contrast to other reports, where

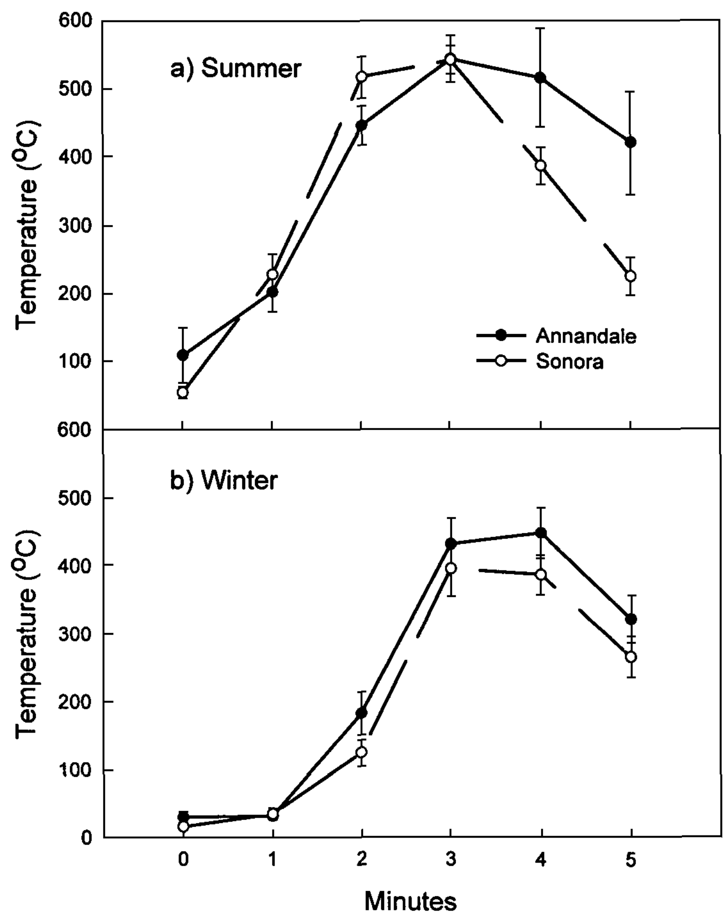

FIG. 5. Temperature profile of 50-g samples of Ashe juniper burned during summer (a) and winter (b). Bars represent ± 1 SE.

little variation was found in the concentration and composition of monoterpenoids between different populations of a single species, including Ashe juniper (Adams and Turner, 1970), Scots pine (*Pinus sylvestris L.*) (Nerg et al., 1994), or alerce (*Fitroya cupressoides* D. Don) (Cool et al., 1991). Our populations of trees were geographically distant (about 120 km apart), and we hypothesize that the greater concentrations found on the Sonora site resulted from environmental differences between Sonora and Annandale. Precipitation was sporadic at both sites, but the Annandale site received more precipitation on average than

TABLE 1. REGRESSION COEFFICIENTS OF BANDED MAIN DIAGONAL MODEL OF PLANT FLAMMABILITY ASSOCIATED WITH PLANT AND SITE CHARACTERISTICS

Factor	Regression coefficient	Standard error	*t* value	*P*
Site	4.84	1.81	2.67	0.011
Tree sex	−3.87	1.51	−2.57	0.021
Camphor	−0.1	0.46	−0.22	0.828
Bornyl acetate	−2.08	0.47	−4.42	0.001
Limonene	6.78	1.57	4.30	0.001
Energy content (wet weight basis)	0.03	0.04	0.84	0.45
Gravimetric plant moisture	0.37	1.65	0.22	0.83
Energy content (dry weight basis)	0.002	0.02	0.11	0.92

Sonora over the 16 months of this study (5.9 vs 3.3 cm/month, Figure 3C). The trees at Sonora responded to the lower precipitation by exhibiting greater water stress (e.g., lower xylem water potential) than the trees at Annandale (Figure 3B). Drought stress has been shown to increase the concentrations of monoterpenoids in other coniferous species (Kainulainen et al., 1992; Gilmore, 1977) and may have increased the concentration in the Sonora trees. Other environmental factors, such as soil fertility, may have affected monoterpenoid concentrations (Muzika et al., 1989) but could not be investigated in this study. Ashe juniper is a drought-tolerant species that can access soil moisture, and presumably nutrients, from the fractured limestone bedrock. During prolonged dry periods, Ashe juniper remains photosynthetically active and transpires water even though surface soils are completely dry (Owens and Schreiber, 1992), which indicates that deeper sources of water within the substrate are being tapped.

Most monoterpenoids (12 of 14) exhibited seasonal differences in concentration with the greatest concentrations in the winter and spring. Riddle et al. (1996), on the other hand, found the greatest concentrations of monoterpenoids in Ashe and redberry juniper (*J. pinchottii*) in the spring and the least concentrations in the winter. The season of peak concentrations seems to be species-specific with reports of spring maximums for Scots pine and some junipers (Adams, 1970) and summer maximums for Douglas fir (Gambliel and Cates, 1995; Zou and Cates, 1995), rubber rabbitbrush [*Chrysothamnus nauseosus* (Pursh) Britt.] (Halls et al., 1994), and other coniferous species (Wagner et al., 1990). Monoterpenoid content at the lowest concentrations may be under genetic control (Welch and McArthur, 1981; Adams, 1970), while the environment controls the monoterpenoid content at other times.

Flammability. Extracting ether-soluble substances (including monoterpenoids) from flammable Mediterranean shrubs can decrease flammability by increasing time to ignition, raising ignition temperature, decreasing flaming time, and decreasing flame height and intensity (Montgomery, 1976). The extracted material contains about twice the heat content of the remaining fuel (Philpot, 1969), and heat content has been shown to positively affect plant flammability (Rodríguez Añón et al., 1995). In our case, the percentage of the plant that burned was dependent not only on the heat content on a fresh weight basis but also by the concentration of specific monoterpenoids (Table 1). As the concentration of limonene increased during the fall and late winter (Figure 2), plant flammability increased (Figure 4). Flammability did not increase at the maximum linear rate because the concentration of bornyl acetate was increasing at the same time. Bornyl acetate has a net negative effect on flammability. Limonene naturally occurs in a liquid state and has a boiling point of 80°C, whereas bornyl acetate occurs as a crystal and has a boiling point of 107°C. The higher boiling point and crystal structure of bornyl acetate implies a greater volatilization temperature, and hence a lower degree of flammability.

The seasonal pattern of plant flammability was best modeled using a banded main diagonal variance/covariance matrix. The variance estimate was least when a large percentage of the plant burned and greatest when the plants were not very flammable (Figure 4). The narrow range of responses of plant flammability suggests that the environment may be regulating flammability when the plants are stressed (Figures 3B and 4). The much greater range of responses seen when plants are less stressed (e.g., greater xylem water potentials) indicates that characteristics of individual plants are regulating flammability under unstressed conditions. This model also allowed the covariance to change according to the sampling period, which suggests that the percentage of the plant that burned during any sample was independent of the amount that burned during another time of the year. This supports other observations that plant flammability changes seasonally.

The concentration and composition of monoterpenoids in plant tissue has been used extensively to separate species taxonomically via chemosystematics (Adams, 1977, 1994; Adams et al., 1984), to explain plant defenses against herbivory (Raffa and Smalley, 1995; Zou and Cates, 1995; Duncan et al., 1994), and to describe altered ecosystem processes such as nutrient cycling (White, 1994). Monoterpenoids may also play an additional role in plant communities by altering plant flammability (Bond and Midgley, 1995; Zedler, 1995). A current hypothesis suggests that being flammable may benefit a species if resultant fires kill neighboring nonflammable plants and increase the fitness of the flammable species (Bond and Midgley, 1995). Ashe juniper does not support this hypothesis because, although flammability changes, neighboring species are resprouting shrubs and grasses, which are rarely affected by fires (Reineke, 1996). Fitness is not increased because most Ashe juniper seedlings and most of the seed bank occur under the canopy of mature trees (Owens and Schliesing, 1995), so fires can selectively remove Ashe juniper from the plant community. It would appear that flammability on an individual level has developed in conjunction with tolerance to other stresses such as herbivory and water stress (Troumbis and Trabaud, 1989).

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