A soluble enzyme preparation from immature sage (Salvia officinalis) leaves has been shown to catalyze the cation-dependent cyclization of geranyl pyrophosphate to the isomeric monoterpene olefins (±)-α-pinene and (−)-β-pinene and to lesser amounts of camphene and limonene (Gambliel, H., and Croteau, R. (1982) J. Biol. Chem. 257, 2335–2342). This preparation was fractionated by gel filtration on Sephadex G-150 to afford two regions of enzymic activity termed geranyl pyrophosphate:pinene cyclase I (Mₐ ≈ 55,000), which catalyzed the conversion of geranyl pyrophosphate to the bicyclic olefin (±)-α-pinene, and to smaller quantities of the rearranged olefin (+)-camphene and the monocyclic olefin (±)-limonene, and geranyl pyrophosphate:pinene cyclase II (Mₐ ≈ 96,000), which transformed the acyclic precursor to (−)-α-pinene and (−)-β-pinene, as well as to (+)-camphene, (−)-limonene, and the acyclic olefin myrcene. The multiple olefin biosynthetic activities co-purified with pinene cyclase I on four subsequent chromatographic and electrophoretic steps, and the ability to cyclize geranyl pyrophosphate and the related allylic pyrophosphates neryl pyrophosphate and linalyl pyrophosphate was likewise coincident throughout purification. Fractionation of pinene cyclase II by an identical sequence showed that the activities for the synthesis of the stereocinetically related (−)-olefins co-purified, as did the ability to utilize the three acyclic precursors. The general properties of cyclase I and cyclase II were determined, and a scheme for the biosynthesis of the pinenes and related monoterpene olefins was proposed.

The volatile oil of immature sage (Salvia officinalis) leaves contains (±)-α-pinene and (−)-β-pinene as the major bicyclic monoterpene constituents, and (±)-camphene, (±)-limonene, terpinolene, and myrcene as lesser olefinic components (Fig. 1), and soluble enzyme preparations from this tissue were recently shown (1) to catalyze the divergent cation-dependent cyclization of the acyclic C₁₀ precursor [1-³H]GPP¹ to (±)-[7-³H]α-pinene and (−)-[7-³H]β-pinene, and to lesser amounts of the other monoterpene olefins. The possibility of isomerization of β-pinene to α-pinene was eliminated, as was the involvement of other free intermediates in the cyclization. Thus, GPP was converted, without detectable intermediates, to the mixture of pinene isomers and other olefins in spite of the fact that this allylic pyrophosphate cannot cyclize without prior isomerization of the trans-double bond at C-2. The related allylic pyrophosphate isomers NPP and LPP (Fig. 1), for which no steric obstruction to direct cyclization exists, could also function as acyclic precursors of the pinenes and of the other monoterpene olefins, although the product mixture in both cases differed somewhat from that generated from GPP (1). The cyclization of the various acyclic precursors was accomplished without detectable interconversion among them, and earlier studies with [1-³H,U-¹⁴C]GPP had ruled out possible isomerization schemes based on initial oxidation at C-1 of GPP (2).

The co-occurrence in the same species of the (+)- and (−)-modification is fairly common among the cyclic monoterpenes (3–5) but rare among the higher terpenes (6–8), and it is generally assumed that such enantiomers are synthesized independently via stereochemically distinct routes. In the present instance, the labeling patterns of the (+)-(1R,5R)- and (−)-(1S,5S)-pinenes derived from [1-³H]GPP are consistent with the generation of the pinane nucleus from the respective (±)-(4R) and (−)-(4S)-monocyclic α-pinanyl intermediates (as originally proposed by Ruzicka et al. (9)), thus implying two in teto stereochemically distinct pathways rather than generation of both antipodes via 1,3-hydride shift in a common bornyl intermediate followed by rearrangement (1). The present cell-free system is the first in which the biosynthesis of enantiomeric terpenes has been demonstrated, and tentative evidence based on differential inhibition and thermal inactivation studies, as well as the response of the activities to pH, have suggested the presence of more than one pinene cyclase activity in this crude preparation (1). Thus, preliminary findings have provided a unique opportunity to examine the biosynthesis of isomeric and enantiomeric terpenes from their allylic pyrophosphate precursors. In this

¹ The abbreviations used are: GPP, pyrophosphate ester of geraniol (3,7-dimethyl-2-trans,6-dienol); NPP, pyrophosphate ester of nerol (3,7-dimethyl-2-cis,6-dienol); LPP, pyrophosphate ester of linalool (3,7-dimethyl-1,6-dien-3-ol); CC, column chromatography; TLC, thin layer chromatography; GLC, gas-liquid chromatography; DEAE, 0-dimethylaminomethyl; MES, 2-[(N-morpholino)-ethanesulfonic acid; Tricine, N-[2-hydroxy-1,1-bis(hydroxymethyl)ethyl]glycine. The systematic names of the monoterpenes have been provided elsewhere (1).
communication, we describe the separation of a (+)-pinene cyclase from a (-)-pinene cyclase and the partial purification and characterization of these unusual enzymes which, in addition to the enantiomeric pinenes, appear to synthesize the configurationally related stereoisomers of camphene and limonene.

**EXPERIMENTAL PROCEDURES AND RESULTS**

**Separation of Olefin Cyclases**—Previous studies have shown that soluble enzyme preparations from sage leaves could cyclize GPP to (+)-α-pinene and (-)-β-pinene and to lesser amounts of camphene and limonene (1). These cyclic olefins are all natural constituents of the oil of sage, as is the acyclic olefin myrcene which is also formed as a minor enzymic reaction product from GPP. Subsequent studies have since revealed that the bicyclic rearranged olefin camphene occurs in sage oil as a mixture of (+)- and (-)-isomers (80% (+)-isomer), as does the monocyclic olefin limonene (55% (-)-isomer). Preliminary examination of the properties of the crude enzyme system, as well as stereochemical considerations arising from the natural co-occurrence of both (+)- and (-)-enantiomers of the olefins in sage oil, led to the suggestion that more than one cyclase was present in the preparation (1). To examine this possibility in greater detail, the 105,000× g supernatant from a sage leaf homogenate was concentrated and subjected to preliminary fractionation by gel permeation chromatography on Sephadex G-150 followed by assay of column fractions with [1-3H]GPP as substrate. This procedure allowed the separation of two GPP:olefin cyclase activities (Fig. 2). The higher molecular weight activity (eluting at 1.3 void volumes and designated cyclase I) was shown by radio-GLC (Fig. 3A) to convert the acyclic precursor to α-pinene and to lesser quantities of camphene and limonene. The low level of radioactivity eluting slightly after β-pinene in Fig. 3, A and B, is due to sabinene, for which there is no internal standard. The GPP:sabinene cyclase activity, which elutes on Sephadex G-150 near the cyclase I region, has recently been described (37). This activity is apparently removed on further fractionation, and an association with cyclase I now seems unlikely. The lower molecular weight activity (eluting at 1.7 void volumes and designated cyclase II) was similarly shown to convert GPP to both α- and β-pinene and to lesser quantities of camphene, limonene, and myrcene (Fig. 3B). GPP was also converted to trace levels of terpinolene by cyclase II.

When column fractions were assayed with either [1-3H]NPP or [1-3H]LPP as substrate, a similar pattern of olefin cyclase activities was observed (i.e. the positions of cyclase I and II were identical with those observed with GPP, but the mixture of olefins produced from each acyclic precursor differed somewhat). The relative amounts of olefins derived from GPP (or generated from the other acyclic precursors) by the respective cyclase activities separated by gel permeation chromatography did not vary appreciably in subsequent studies with these types of preparations, but the levels of cyclase I and cyclase II in a given preparation were shown to vary considerably with plant growth conditions. Thus, plants raised in the greenhouse under the lower light intensity and short photoperiod of the winter months contained relatively low proportions of cyclase I activity. For this reason, constant growth conditions (1) were maintained throughout the course of the investigation.

**Stereochimeristry and Labeling Pattern of the Biosynthetic Products**—Since both cyclase activities produced similar sets of olefins and sage oil is known to contain significant quantities of both enantiomers of these olefins (with the exception of β-pinene which is essentially optically pure), it was of considerable interest to examine the stereochemistry of the biosynthetic products formed by cyclases I and II.

Separation of the α-pinenes from the biosynthetic olefin mixtures produced by the respective cyclases, followed by
stereospecific conversion of each to fenchone xime and separation of the corresponding diastereomeric (−)-menthylmethyl ethers by the procedures described previously (1, 38), revealed cyclase I to produce only (+)-α-pinene and cyclase II to produce solely (−)-α-pinene. Similar attempts to resolve the biosynthetic camphenes and limonenes by separation of diastereomeric derivatives of the respective derived ketones camphenilone and carvone (as the derived nopinone semicarbazones (30, 31)) and limonenes (as the (+)- and (−)-limonene tetrabromides (34)), the results in Table I indicating that cyclase I synthesizes the (+)-series of olefins and cyclase II the (−)-series. As previous studies have shown that the β-pinene produced by the crude cell-free system was essentially pure (−)-1S:5S)-β-pinene (1), the corresponding product of cyclase II was necessarily this stereoisomer, and this point was confirmed by preparation and crystallization of the derived nopinone semicarbazone. Thus, each product of the respective set exhibits the same absolute configuration at the center derived from C-6 of GPP (i.e. the isopropylidene-substituted carbon) (Fig. 1). This stereochemical relationship appears more than coincidental and suggests that cyclase I and cyclase II are responsible for cascades of olefin cyclizations of opposite enantiomeric specificity. The labeling patterns of the isolated (+)-α-pinene, (−)-α-pinene, and (−)-β-pinene derived from [1-3H]geranyl pyrophosphate were also examined by the methods employed previously, which involve acid-catalyzed rearrangement of the olefin to borneol, oxidation to camphor, and vigorous base-catalyzed exchange of both exo- and endo-α-hydrogens of this partially racemized ketone (1). These results, when corrected...
Radiochemical fractional crystallization of derivatives of the monoterpene olefins derived from cyclase I and cyclase II

<table>
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<tr>
<th>Crystal-</th>
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<tr>
<td>Crystalliz-</td>
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[a]D 69°C 68-69°C 104-105°C 105°C 224°C 225°C 69°C 69 105°C 105°C 224-225°C 225°C

for racemization, were virtually identical with those reported previously (1), verifying that essentially all of the tritium of each biosynthetic pinene was specifically located on the methylene bridge carbon (C-7). Thus, the stereochemistry and labeling pattern of the products are consistent with the independent generation of the (+)- and (−)-pinene nucleus from the respective (+)-4R- and (−)-(4S)-monocyclic α-terpinyl cation by internal addition to the trisubstituted double bond as originally proposed by Ruzicka (9; see also Ref. 1).

Further Purification of Cyclase I and Cyclase II—These results are discussed in Miniprint.

Differential Inactivation Studies with Cyclase I and Cyclase II—These results are discussed in Miniprint.

Properties of Cyclase I and Cyclase II—The apparent molecular weight of pinene cyclase I, estimated by chromatography on a calibrated Sephadex G-150 column, was 95,000, while pinene cyclase II exhibited a molecular weight of around 55,000. Our attempts at hydrophobic chromatography of the two cyclases indicated that both were rather hydrophobic in nature, while cation and anion exchange chromatography and chromatofocusing suggested that both were anionic proteins with pIs below pH 4.5. There is considerable uncertainty in determining accurate pIs from chromatofocusing elution profiles when operating near the lower pH limit of the gradient where the concentration of Polybuffer is highest (20).

In 50 mM Tricine, 25 mM phosphate or 50 mM MES, 25 mM phosphate buffer, cyclase I exhibited a pH optimum around 6.0 (with one-half maximal activity at pHs 5.6 and 6.5), while pinene cyclase II had an optimum near 7.2 (with one-half maximal activity at pHs 6.8 and 7.8). Earlier studies with the 105,000 X g supernatant from a sage leaf homogenate revealed that the pH curve for α-pine cyclase activity in this crude preparation was bimodal with optima near 6.0 and 7.2, a result now clearly explained as reflecting the optima of cyclase I and cyclase II, respectively.

Diaysis of the preparations to remove divalent cations in the buffer resulted in complete loss of activity of both cyclases (with GPP as substrate), and readdition of 15 mM MgCl₂ resulted in the restoration of more than 90% of the original cyclase activity of both enzymes and for all products. In both cases, MnCl₂ (under saturating conditions) could substitute for MgCl₂, but was only 60 to 70% as effective in restoring total olefin cyclase activity. When the synthesis of individual olefins was examined in response to cation, differential effects were noted. The synthesis of (+)-α-pinene (cyclase I) and (−)-β-pinene (cyclase II) from GPP exhibited saturation at MnCl₂ levels below 2 mM while displaying a preference for MgCl₂ at higher concentrations, whereas the synthesis of (−)-α-pinene (cyclase II) displayed a marked preference for MgCl₂ at all levels tested (Fig. 7) as did the synthesis of camphene by both cyclases (data not shown). Unusual effects of the divalent cation were also observed using other substrates.

Most notable with cyclase II was the combination of LPP and MnCl₂, which afforded abnormally high levels of the acyclic olefin myrcene, as well as cis- and trans-ocimene which are not significant constituents of sage oil. The synthesis of abnormally high levels of acyclic olefins from LPP, now attributable to cyclase II, had been noted earlier in crude preparations containing both cyclases (1). While it is clear from these results that a divalent cation is required for cyclase activity, the nature of the interaction of the cation with the substrate and/or enzyme and the resulting influence on product distribution are not presently understood. It seems likely, however, that Mg²⁺ functions as the required cation in vivo, since in crude preparations containing both cyclases, the product distribution afforded by GPP in the presence of Mg²⁺ is virtually identical with that produced by intact tissue (1).

As indicated previously, both cyclases are inhibited by thiol-directed reagents, and both exhibit greater sensitivity to p-hydroxymercuribenzoate than to N-ethylmaleimide. Both cyclases were also inhibited by low levels of inorganic pyrophosphate (50% inhibition of cyclases I and II at PP concentrations of 0.25 and 0.42 mM, respectively).

While it is preferable to examine the kinetic properties of the cyclases only after removal of all competing activities, it was not possible to routinely remove all residual phosphohydrolase activities by chromatography on DEAE-cellulose. Therefore, substrate hydrolysis was routinely monitored and the appropriate corrections for substrate loss were made. Conversion of the pyrophosphorylated substrates to the inactive monophosphates and free alcohols never exceeded the rate of conversion to cyclic olefins and never represented more than 10% loss of starting material. Earlier studies with unfractionated cell-free systems had shown that NPP as a substrate gave rise to unusually high levels of limonene and terpinolene in addition to the bicyclic products, whereas LPP as a substrate afforded abnormally high levels of myrcene and resulted in the formation of ocimenes (which are not known
to occur in sage oil in any but trace levels (41)). These unusual and, as yet, unexplained effects persisted with the partially purified cyclases, and for this reason only the bicyclic olefins, pinenes and camphene, were examined for comparative purposes. The rates of cyclization as a function of substrate concentration with GPP, NPP, and LPP gave rise to typical hyperbolic saturation curves with all substrates for both cyclases. The double reciprocal plots were linear in all cases, and the measured \( K_m \) values were in the 2.5-4.0 \( \mu M \) range for both cyclases regardless of the substrate. Relative \( V_\text{s} \) determined for both cyclases for GPP, NPP, and LPP were about 1.0, 0.7, and 1.2, respectively. Thus, the two cyclases appear to be quite similar with regard to kinetic constants. Some caution is required in interpreting the results obtained with LPP, however, as this substrate was racemic, and, while it seems safe to assume that only one enantiomer is active with each cyclase, the fate and/or influence of the “inactive” enantiomer is not known. Both inhibition of cyclization of the correct enantiomer and a role in the formation of the abnormal acyclic products could be possible. As in previous studies with this enzyme system, the product mixtures generated from each parent precursor were examined for the presence of geraniol, nerol, and linalool, and their corresponding phosphates and pyrophosphates (1). No evidence was obtained for enzymic interconversion of the acyclic precursors under the conditions of the assay.

**DISCUSSION**

The pinene cyclases resemble other monoterpene cyclases in general properties, such as molecular weights in the 50,000-100,000 range, \( \text{pH} \) optima between 6.0 and 7.5, inhibition by thiol-directed reagents and inorganic pyrophosphate, and a requirement for a divalent cation (42). Both \( \text{Mg}^{2+} \) and \( \text{Mn}^{2+} \) can function in the latter role, although \( \text{Mg}^{2+} \) is preferred at saturating concentrations, and, on the basis of product distribution, would appear to be the cation which operates in vivo. In contrast, \( \text{Mn}^{2+} \) is the preferred cation for pinene synthesis by cyclase preparations from Citrus (43, 44). Both cyclases from sage appear to be rather hydrophobic and to possess relatively low \( \text{pI}s \) (4.5) compared to most proteins (45). Both cyclases are apparently unstable near their \( \text{pI} \).

The results of four-step purification of each cyclase, as well as differential inactivation studies, provide strong evidence that each cyclase synthesizes a set of stereochemically related products (\(+\)-\( \alpha \)-pinene, \(+\)-camphene, and \(+\)-limonene in the case of cyclase I, and \(-\)-\( \alpha \)-pinene, \(-\)-\( \beta \)-pinene, \(-\)-camphene, \(-\)-limonene, and myrcene in the case of cyclase II). A number of earlier reports have described the conversion of acyclic precursors to multiple cyclic products in partially purified systems (26, 43, 44, 46, 47), yet the present report provides the most conclusive evidence to date that multiple products can, in fact, be synthesized by a single monoterpene cyclase.

Both cyclases I and II can utilize GPP, NPP, and LPP as the substrate. This feature is not in itself unusual, as most monoterpene cyclases examined thus far possess the ability to cyclize all three precursors without apparent interconversion among them (42, 48). In some instances significant differences in the efficiency of conversion of GPP, NPP, and LPP to cyclic products have been described in relatively crude cell-free systems (11, 47, 49, 50). Results from this and other recent studies (27, 51) suggest that these earlier observations should be regarded with some caution until product distribution and alternate fates of the substrates are carefully examined. Thus, in the present instance correction for abnormal products derived from NPP and LPP and for differential loss of substrates to competing activities (e.g., phosphohydrolases) revealed relatively little difference between the three precursors in the efficiency of conversion to bicyclic olefins.

The present study, as well as those of others working with related systems (44, 48, 52), have not yet provided a definitive answer regarding the role of free NPP and LPP in monoterpene cyclizations. Nevertheless, any scheme for the conversion of acyclic precursor to the stereochemically related cyclic olefins should account for the observed cyclizations of all precursors, and in particular for the transformation of the likely in vivo progenitor GPP, a compound which, unlike NPP and LPP, cannot cyclize directly, but which clearly does so without the intervention of free intermediates. Such a process must necessarily involve preliminary isomerization to a bound intermediate competent to cyclize; presumably the tertiary allylic linalyl system in which free rotation about C-2-C-3 is permitted. Such a scheme for the isomerization of GPP and the subsequent cyclizations, which is consistent with the available data and based on relevant chemical models (53-58), is illustrated in Fig. 8. Accordingly, GPP ionizes to a stabilized allylic cation, followed by collapse to LPP (or an enzyme linked equivalent) allowing the required rotation about the C-2-C-3 bond of this intermediate. Reionization of the cisoid conformer followed by deprotonation allows formation of acyclic olefins by cyclase II (more likely from the extended conformation (59) rather than the folded conformation illustrated here), whereas intramolecular electrophilic addition to the 6,7-double bond generates the transient \( \alpha \)-terpinyl cation from which \(+\)-limonene (cyclase I) and \(-\)-limonene (cyclase II) are derived by subsequent deprotonation. Alternatively, an additional electrophilic attack on the newly formed cyclohexenoid double bond of the \( \alpha \)-terpinyl system generates either the pinane skeleton, which allows formation of \(+\)-\( \alpha \)-pinene (cyclase I) and, by two options for deprotonation, \(-\)-\( \alpha \)-pinene and \(-\)-\( \beta \)-pinene (cyclase II), or the bornane skeleton (directly, or via the pinane nucleus), which then undergoes Wagner-Meerwein rearrangement to the camphane skeleton from which \(+\)-camphene (cyclase I) and \(-\)-camphene (cyclase II) arise. The extent of participation by the enzyme in these processes can only be conjectural at this point; however, the role of the cyclase is clear in facilitating the elimination of pyrophosphate, stabilizing and directing the intermediate species into the appropriate configurations, excluding water and promoting proton elimination to terminate the reactions. Although covalent intervention (e.g., at the tertiary center of the linalyl system) cannot be precluded at this time, we would, in agreement with well-reasoned arguments based on related enzyme systems (60-62), suggest here that it is the pyrophosphate anion which acts to stabilize the cationic intermediates and additionally may assist in the terminating deprotonations.

Since ionization of the tertiary intermediate generated from GPP is postulated to trigger the cyclization cascade, it is not possible to assign with certainty the configuration of the bound linalyl systems which give rise to the respective anti-podal series of olefins. Yet steric considerations, involving the departure of the leaving group from the face of the allylic system opposite to that which the nucleophilic double bond with side chain becomes attached, as well as the favorable positioning of the counter ion so as to stabilize most of the postulated intervening cationic species, suggest that the \(-\)-3R-linalyl system gives rise to the \(+\)-olefin series and the \(+\)-3S-linalyl system to the \(-\)-olefin series. Similar reasoning has been invoked previously to rationalize the origin of anti-podal bornane monoterpenes (63).

Cyclization through a common enzyme-bound intermedi-
ate, as indicated in Fig. 8, could also explain the cyclization of GPP, NPP, and LPP without interconversion of the free forms, but it is not immediately apparent how this scheme might rationalize the nonequivalence in product formation observed with the different substrate-metal ion combinations. The metal ion-assisted solvolysis of LPP to acyclic olefins might suggest a partial explanation for the phenomenon (52), yet the appropriate controls ensured the enzymatic rather than solvolytic origin of these olefinic products. Additionally, this argument, as well as those based on the uncertain fate of racemic LPP, would apply only to cyclase II. Alterations in the balance between cyclization and elimination processes observed with the three acyclic precursors and two cations could result from differences in the relative orientation of the pyrophosphoryl group and the various terpynyl moieties on initial binding and may involve a role for the metal ion beyond that of assisting in the initial ionization (64, 65). These and related questions regarding the stereochemistry and control of product distribution by these novel enzymes will be the subject of further communications.

Acknowledgments—We thank Richard Hamlin for raising the plants and Jerry Winters for technical assistance.

REFERENCES
The enzymatic conversion of the allylic phosphate substrates to the corresponding monophosphates and free alcohol was monitored under the same conditions used to measure radio-labeled reaction mixtures. The free alcohols from the phosphate extract or alcohols acidified with acetic acid were isolated by liquid chromatography.
Differential Inactivation Studies provide evidence that high concentrations of Polybuffer in the buffer gradient, especially at the low end, resulted in the loss of cyclase activity. This loss was greatly reduced if the preparation was subjected to disc gel electrophoresis under nondenaturing conditions. A single diffuse band migrating approximately one quarter of the way into the gel was observed. Gel filtration of some 50\% of the remaining activity on Bio-Gel P-60 also demonstrated that the enzyme was not covalently modified, but which did nevertheless demonstrate some 10\% of the residual activity.

The coincidence of enantiomeric cyclase activities from either of the three acyclic substrates could be demonstrated by assaying the suspended gels directly for cyclase activity.

The inhibition of cyclase activity by high concentrations of Polybuffer in the buffer gradient, especially at the low end, resulted in the loss of cyclase activity. This loss was greatly reduced if the preparation was subjected to disc gel electrophoresis under nondenaturing conditions. A single diffuse band migrating approximately one quarter of the way into the gel was observed. Gel filtration of some 50\% of the remaining activity on Bio-Gel P-60 also demonstrated that the enzyme was not covalently modified, but which did nevertheless demonstrate some 10\% of the residual activity.
Pinene cyclases I and II. Two enzymes from sage (Salvia officinalis) which catalyze stereospecific cyclizations of geranyl pyrophosphate to monoterpene olefins of opposite configuration.
H Gambriel and R Croteau


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