Garlic-like but Odorless Plant *Allium ampeloprasum* ‘Mushuu-ninniku’


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Summary

We tried to identify the unidentified *Allium* plant, ‘Mushuu-ninniku’, which resembles garlic (*A. sativum* L.) but has no garlic odor. ‘Mushuu-ninniku’ is much larger than a garlic. Its plant height and bulb weight are twice that of garlic. It develops many different sized cloves, inflorescences, and flowers, but no inflorescent bulbil. The chromosome number of ‘Mushuu-ninniku’ is 2n=32, similar to leek (*A. ampeloprasum* L.), but double that of garlic. In restriction fragment length polymorphisms (RFLPs), ‘Mushuu-ninniku’ produced patterns similar to those of leek and quite unlike those of great-headed garlic (*A. ampeloprasum* L.), which usually has a prominent bulb similar to ‘Mushuu-ninniku’. Isozyme analyses also showed some similarity between ‘Mushuu-ninniku’ and leek. Although the alliiinase mRNA size (1.9 kb) of ‘Mushuu-ninniku’ was identical to those of other *Allium* plants examined, the N-terminal 25 amino acids sequence of ‘Mushuu-ninniku’ alliinase was different from those of other *Allium* plants examined except leek. From these results, we concluded that ‘Mushuu-ninniku’ belongs to *Allium ampeloprasum*.

Key Words: *Allium ampeloprasum*, garlic, leek, Mushuu-ninniku, odorless.

Introduction

The vegetables that belong to the genus *Allium* are known to have many pharmaceutical usages in addition to their great value as a spice (Jones and Mann, 1963a; Fenwick and Hanley, 1985a; Reuter et al., 1996). A number of papers have described garlic (*A. sativum* L.) as possessing these properties afforded by various sulfur compounds, such as S-allyl cysteine sulfoxide (alliin), S-allyl cysteine, diallyl thiosulfinate (alliicin), allyl methyrl trisulfide, and ajeneine (E,Z)-4,5,9-trithiadodeca-1,6,11-triene 9-oxide, (Fenwick and Hanley, 1985b; Reuter et al., 1996; Ariga et al., 1981; Apitz-Castro et al., 1983). These compounds have an unique, strong odors, except for a few cysteine derivatives such as alliin or S-allyl cysteine. Some people find the odors to be extremely pungent. To reduce the level of such odors, many “odorless garlic” products have recently been developed and sold. These products are derived from two groups: garlic bulbs, which have been changed into an odorless or odor-minimized powder, paste, or sliced and dried tips; and garlic-like but odorless bulbs.

Currently, the sole cultivar that supplies this type of bulbs in Japan is the ‘Mushuu-ninniku’ or ‘Jumbo-ninniku’ or ‘Shiro’. ‘Mushuu”, “ninniku” and “Shiro” are Japanese words meaning odorless, garlic, and white, respectively.

Since pharmaceutical properties of garlic have been attributed to the above sulfur compounds, the question arose as to whether ‘Mushuu-ninniku’ possesses compounds with properties comparable of the common garlic, both qualitatively and quantitatively. Moreover, it is uncertain whether or not ‘Mushuu-ninniku’ belongs to garlic. In this study, we sought to classify ‘Mushuu-ninniku’ according to its morphological and biochemical characteristics, compared with those of other related species, garlic, leek (*A. ampeloprasum* L., Leek group), great-headed garlic (*A. ampeloprasum* L., Great-headed group), and onion (*A. cepa* L.).

Materials and Methods

Plant Materials

A plant of ‘Mushuu-ninniku’ was obtained from a farm which introduced it, from Toyama Prefecture. Samples of garlic ‘Fukushi-howaito’, leek ‘American Flag’ and onion ‘O.K-ki’ were gifts from Kawada...
Food Co., Tokyo, whereas the 'Ishu-wase' was purchased from Sakata Seed Co., Yokohama, and 'California Late' and 'California Early' were gifts from the Bureau of Upland Field Crops, Saga Prefectural Agriculture Research Center, Saga. Garlic strains No. 184 and No. 321 were obtained from a local market in Tashkent, Uzbekistan, and Zagreb University, Croatia, respectively. The great-headed garlic 'Elephant' was obtained from Michigan, USA. Leek strains No. 34 and No. 27 were from van der Meer, Q.P. (Netherlands).

Chromosome analysis

Chromosomes of 'Mushuu-ninniku' were analyzed by the method of Konvicka and Levan (1972), and compared with those of other plants. Briefly, fresh root tips were immersed in 20 volumes of 1% colchicine for 6 hr, fixed with 45% acetic acid for 30 min at 10°C, then treated with 1N HCl:45% acetic acid at 60°C for 15 sec to split cell-to-cell junctions. The tips were then transferred onto a slide glass and treated with 1-2 drops of 1% aceticarmine solution. After having been covered with a cover glass, the slide was placed on several sheets of wet gauze on a hot plate at 60°C and kept there for 10 min. The cover glass was then pressed with a finger to make the cells a monolayer; the preparation observed microscopically.

Extraction of total RNA

RNA was extracted by the method of Finkelstein and Crouch (1986) with some modification. Ten grams of well-developed cloves or the elongated foliage leaf-bases in the case of leek were frozen in liquid nitrogen and then pulverized to a powder, which was suspended in a combined solution of 15 ml of 0.1 M Tris-HCl buffer (pH 9.0), containing 0.1 M NaCl, 1% SDS and 15 ml of phenol, chloroform and isoamyl alcohol (25:24:1, v/v/v). The suspension was shaken vigorously for 5 min, and centrifuged at 4,500 g for 15 min at room temperature. The water layer was treated twice with the same volume of the organic solvent and the precipitation of RNA with ethanol were carried out according to Galau et al. (1981).

Preparation of genomic DNA

A 20-g samples of frozen cloves or leaf-bases were freeze-dried and pulverized in a mortar. To the powder, 50 ml of 0.7 M NaCl, 50 mM Tris-HCl (pH 8.0) containing 1% cetyltrimethylammonium bromide, 0.54 mmol EDTA and 0.5 mmol 2-mercaptoethanol were added. The suspension was incubated at 55°C for 1 hr. Subsequent procedures for DNA isolation and ethidium bromide labeling as well as its precipitation were performed according to Pavloksi et al. (1994).

Restriction fragment length polymorphism (RFLP) analysis of total DNA

The RFLP analysis of the total DNA was done according to Tsuneoishi et al. (1992), using two probes, #65-3 (4.8 kb) and #8-3 (3.7 kb), derived from garlic mitochondrial DNA in combination with two restriction enzymes, EcoRI and Hind III. The hybridization between these probes and the DNA digests was carried out by employing the "universal probe system" developed by Nakagami et al. (1991).

Purification of alliinase

Aliinase (C-S-lyase or alliin lyase, E.C. 4.4.1.4) was purified from plant extracts through the procedures of Nock and Mazelis (1986) and Lohmuller et al. (1994). All purification steps were performed at 4°C; the alliinase activity was monitored by the method of Jansen et al. (1989), using S-allyl-L-cysteine sulfoxide as a substrate.

'Mushuu-ninniku' alliinase: One kg of cloves was homogenized in 2 liter of 0.02 M phosphate buffer (pH 7.0) in a blender. The homogenate was filtered through a cotton gauze, and the filtrate centrifuged at 16,500 g for 60 min. The proteins in the supernatant were subjected to ammonium sulfate precipitation at 65% saturation; the precipitate, which was centrifuged at 16,500 g for 30 min, was dissolved in 200 ml of the phosphate buffer and then dialyzed against the same buffer for 18 hr. The dialyzed solution was applied onto a hydroxyapatite column (50 mm, i.d x 200 mm) equilibrated with 0.02 M phosphate buffer (pH 7.0). The alliinase fraction was eluted by increasing the buffer concentration to 0.2 M phosphate. After dialysis against 20 mM acetate buffer (pH 5.0) for 4 hr, the alliinase fraction was applied onto a Hi-Trap SP column (5 mm i.d. x 30 mm, Amersham Pharmacia Biotech, Inc., Tokyo), which had been equilibrated with 0.31 M NaCl in 20 mM acetate buffer (pH 5.0), and eluted by increasing the NaCl concentration up to 0.5 M. At the final step of purification, the alliinase was gel filtered through a Superdex 200 pg column (16 mm x 600 mm, Amersham Pharmacia Biotech, Inc.). For the gel filtration, the active fraction was dialyzed for 12 hr against 0.02 M phosphate buffer (pH 7.0) containing 0.15 M NaCl, and then applied onto the column equilibrated with the phosphate buffer. Alliinase, eluted from the column, was concentrated by ultra filtration.

Alliinases from other related Allium plants: Purification of alliinases was performed as described above, except for the step of the cation exchanger adapted for 'Mushuu-ninniku'. In place of the cation exchanger, a concanavalin-A agarose (ConA) column (Amersham Pharmacia Biotech, Inc.) and a butyl Toyo-pearl (BTP) column, a hydrophobic one (Toso Co., Tokyo), were used to purify garlic and great-headed garlic alliinases, respectively. Garlic alliinase was eluted from a ConA column with 50 mM methyl mannos. Great-headed garlic alliinase was obtained as a pass-through fraction of a BTP column, which was equilibrated with 0.02 M phosphate buffer (pH 7.0) containing 0.3 M ammonium sulfate.
Analysis of isozymes

Extraction of isozymes: Protein fractions containing enzymes were extracted at 4 °C by the method of Nock and Mazelis (1986) with some modification. Briefly, bulbs of 'Mushhu-ninniku', garlic, great-headed garlic, onion, and thickened bases of leaf sheaths of leek were extracted by soaking 100-g samples in 150 ml of 0.02 M phosphate buffer (pH 7.0), containing 20 μM pyridoxal-5-phosphate, 10% (v/v) of glycerol, 1 mM phenylmethylsulfonyl fluoride, 5% (w/v) of NaCl, 5 mM EDTA, 5% (w/v) polyvinylpyrrolidone, and 0.05% (v/v) of 2-mercaptoethanol; then homogenizing in a blender for 5 min. Proteins in the homogenate were precipitated by ammonium sulfate at 65% saturation. After standing for 1 hr, the precipitate was pelleted by centrifugation for 30 min at 16,500 g, dissolved in 0.02 M phosphate buffer (pH 7.0), and the solution was dialyzed against the phosphate buffer for 18 hr. The resulting protein solution was subjected to the isozyme analysis, by isoelectric focusing and enzyme staining.

Ieoelectric focusing: The isoelectric focusing of the above proteins was carried out on a polyacrylamide gel plate containing Ampholine (Amersham Pharmacia Biotech Inc.). For glucose-6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49) and alliinase, the gels were run at pH 3.5–9.5 and pH 4.0–6.5, respectively. These gel plates were pre-electrolyzed for 1 hr before loading the samples, and then electrolyzed further at 1 mA cm⁻¹ width for 2 hr. G6PDH was stained as described by Wetter and Dyck (1983) and Vallejos (1983). Alliinase was stained according to Yoshikawa et al. (1994), using N-allyl-L-cysteine sulfoxide as a substrate.

Methods for other analyses

SDS-PAGE was carried out by the method of Laemmli (1970). Amino acid sequences of the alliinase samples were determined by using a sequenator (477A, Perkin-Elmer Co., Conn., USA). Northern blot analysis was carried out by using a 32P-labeled probe prepared by the random primer technique from the garlic alliinase cDNA (1470 bp) provided by Dr. Van Damme, E. of the Katholieke Universiteit, Leuven, Belgium (Van Damme et al., 1992).

Results

Morphological characteristics of ‘Mushhu-ninniku’

The outward morphology of ‘Mushhu-ninniku’ is similar to that of garlic (Fig. 1). The most conspicuous difference between the two is in their sizes; ‘Mushhu-ninniku’ plant is much taller, the distance from the bottom of the bulb to the top of the inflorescence is more than 1.2 m under usual culture conditions, and the bulb weighs about 160 g (Table 1). Some measurable parameters indicate that ‘Mushhu-ninniku’ is not only larger than garlic, it is the most robust types of Allium plants

<table>
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<th>Plant material</th>
<th>Bulb</th>
<th>Clove</th>
<th>Bulblet</th>
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<tr>
<td></td>
<td>Weight</td>
<td>Diameter</td>
<td>Weight</td>
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<td>Garlic 'F-h'</td>
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<td>6.2 ± 0.2</td>
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<tr>
<td>'Mushhu-ninniku'</td>
<td>156.5 ± 54.3</td>
<td>9.1 ± 0.7</td>
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* A bulb of 'Mushhu-ninniku' consisted of large stem-attached cloves (more than 10 g), surrounded by smaller cloves ranging from 10 g to 0.1 g and bulblets.
* 'F-h' = 'Fukuchi-howaito'
developing numerous cloves, ranging from 24 g to 0.1 g, composing a single bulb. Morphologically, 'Mushuu-ninniku' is also distinctive from garlic, having several bulblets surrounding a main bulb (Table 1) and a well-developed inflorescence lacking bulbils (Table 2). The structures of the bulb, umbel, and flower of a plant of 'Mushuu-ninniku' (Figs. 2 and 3) are very similar to those of great-headed garlic.

**Chromosomes of 'Mushuu-ninniku' and other related Allium plants**

The somatic chromosome number in 'Mushuu-ninniku', which was counted at the mitotic metaphase of root tip cell nuclei, was determined to be $2n=32$, identical with that in leek (Levan, 1940; Jones and Mann, 1963b). Those of garlic 'Fukuchi-howaito' and onion 'O.K.-kii' are $2n=16$ (Konvicka and Levan, 1972; Verma and Mittal, 1978), or half that of the 'Mushuu-ninniku'. The chromosome number in great-headed garlic 'Elephant' was determined to be $2n=48$ (Table 3).

**RFLP analysis of total DNA**

The RFLP patterns, derived from the total DNAs of 'Mushuu-ninniku', garlic, leek, great-headed garlic and onion (Fig. 4), using probe #65-3 and the restriction enzyme EcoRI, revealed that the pattern of 'Mushuu-ninniku' was almost similar to those of leek strains (leek - 34 and leek - 27), but quite distinct from those of garlic cultivars (Fig. 4A, left panel). All garlic cultivars shared the bands about 14.2 kb or 9.7 kb or both, but they were

| Table 2. Differences in inflorescence morphology between garlic and 'Mushuu-ninniku'. |
|-----------------------------------|---------------------------------|-----------------|-----------------|
| Plant material                     | Flower color  | Shape of inflorescence       | Bulbil        |
| Garlic                            | lavender      | small and non-globular       | present       |
| 'Fukuchi-howaito'                 | white to purple | large and globular           | absent        |

| Table 3. Chromosome numbers of 'Mushuu-ninniku' and related Allium plants. |
|-----------------------------------------------|-----------------|
| Plant material                  | Chromosome number ($2n$) |
| 'Mushuu-ninniku'                     | 32              |
| Garlic                              | 16              |
| Leek                                | 32<sup>2</sup>  |
| Great-headed garlic                | 48              |
| Onion                               | 16              |

<sup>2</sup> Levan (1940).

**Fig. 2.** Morphologies of bulbs of 'Mushuu-ninniku' and garlic cv. 'Fukuchi-howaito'. (A) The bulb size of 'Mushuu-ninniku' (A, left) is double or more than that of garlic (A, right); usually 'Mushuu-ninniku' has numerous bulblets surrounding the encased main bulb with thick involucral leaf skin. (B) Cross-sections of 'Mushuu-ninniku' and garlic bulbs, showing the presence of bulblets around the main bulb, but also in the structure within the bulb as compared with garlic. The 'Mushuu-ninniku' cloves are located in an irregular arrangement around the scape. Garlic cloves tend to be located regularly around the scape, although there are many cultivars having the cloves arranged irregularly. (C) The bases of the 'Mushuu-ninniku' and garlic bulbs. The base of 'Mushuu-ninniku' bulb, which has numerous roots, is dignified similar to that of garlic, but it is characteristically 3 times larger than that of garlic. Bars=5 cm.
undetectable in ‘Mushuu-ninniku’. Although onions did not produce any band under these conditions, the great-headed garlic produced a few bands of less than 7.2 kb, which were similar to those of the garlic ‘Ishu-wase’, but distinct from those of leek strains and ‘Mushuu-ninniku’. With the same probe, HindIII digests of ‘Mushuu-ninniku’ DNA showed a pattern identical with those of leek strains (Fig. 4A, right panel). Four cultivars of garlic produced patterns different from each other, but none were comparable to that of ‘Mushuu-ninniku’.

With probe, #8–3, the EcoRI digests of DNAs from all five garlic cultivars produced a common fragment length of 1.9 kb, discriminating these cultivars from ‘Mushuu-ninniku’ and other species (Fig. 4B, left panel). From these results, it is evident that ‘Mushuu-ninniku’ is not a garlic and belongs to some other species. This probe/enzyme system exhibited a fragment length pattern of ‘Mushuu-ninniku’ similar to, but not identical with those of leek strains. However, the probe #8–3 hybridized with HindIII digests at a position common to most of the Allium plants examined, excluding great-headed garlic and onion which were not hybridized with this probe (Fig. 4B, right panel). These RFLP analyses reveal that leek and ‘Mushuu-ninniku’ which have similar RFLP patterns, may be genetically closely related to plants belonging to A. ampeloprasum.

Allinase gene expression in ‘Mushuu-ninniku’

The 1.9 kb mRNA (Fig. 5) was detected in every Allium plant examined. Garlic expressed more allinase mRNA than the others, demonstrating that garlic has the highest potency for producing volatile compounds, whereas ‘Mushuu-ninniku’, which has a lesser amount of allinase mRNA, might generate less volatiles.
Comparison of amino acid sequences of alliinases between 'Mushuu-ninniku' and other related Allium plants

'Mushuu-ninniku' alliinase showed a sequence identical with that of leek alliinase (Fig. 6), whereas alliinases from garlic, onion, and great-headed garlic possessed 2–4 different amino acids. Thus, great-headed garlic alliinase is the farthest from 'Mushuu-ninniku' in amino acid sequence. Every different amino acid from its counterpart was derived from a single base change in each RNA codon.

Comparison of isozymes between 'Mushuu-ninniku' and other related Allium plants

Zymograms, reflecting the alliinase activity, were quite different among the species (Fig. 7). The isozyme pattern of 'Mushuu-ninniku' alliinase was distinct from those of garlic, onion, and great-headed garlic. The bands that migrated at around pH 8.1 were similar to those of leek. The patterns of G6PDH isozymes were similar among Allium plants examined (Fig. 8); those of 'Mushuu-ninniku' were closest to patterns of onion and leek. These isozyme analyses demonstrate that 'Mushuu-ninniku' has similar enzymatic phenotypes as leek, but is distinct from those of garlic and great-headed garlic.

![Northern blot analysis](image)

**Fig. 5.** Northern blot analysis of the alliinase mRNAs isolated from 'Mushuu-ninniku' (Mu); garlic 'Fukuchi-howaito' (G); onion 'O.K.-kii' (O); great-headed garlic 'Elephant' (Gh).

![Zymograms](image)

**Fig. 7.** Zymograms of alliinase isozymes in 'Mushuu-ninniku' and related Allium plants. Leek 'American Flag' (L). For other letters see legend on Fig. 5.

| Amino terminal sequence of alliinase from 'Mushuu-ninniku' and those from related Allium plants. 
| For representing the sequence of alliinases from garlic, great-headed garlic and onion, only the amino acids different from those from 'Mushuu-ninniku' or leek are shown with their numbers. |

| NH3- | K | V | T | W | F | M | A | E | E | A | E | A | Y | V | A | N | I | C | S | G | H | O | R- COOH |
| 1   | 2 | 5 | 10 | 15 | 20 | 25 |

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<th>Onion 'O.K.-kii'</th>
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Some morphological characteristics of ‘Mushhu–ninniku’ were found to be more similar to those of *A. ampeleoprasum*, e.g., leek and great-headed garlic, than to those of garlic. According to the description of Jones and Mann (1963b), this species includes three groups, i.e., great-headed garlic group, leek group and kurrat group. Although, ‘Mushhu–ninniku’ might belong to one of these groups or to wild types of these plants, its identity is still obscure by our present morphological observation. In addition, ‘Mushhu–ninniku’ has an onion–like odor and not that of garlic. Thus, the biochemical characters were compared among ‘Mushhu–ninniku’, garlic, great-headed garlic, leek, and onion.

The most decisive coincidence between ‘Mushhu–ninniku’ and leek was their chromosome numbers, which were 2n=32, whereas other plants were clearly different. On RFLPs, ‘Mushhu–ninniku’ DNA produced a pattern similar to, but not identical with that of leek DNA; great-headed garlic DNA was quite different from those of ‘Mushhu–ninniku’ and leek. Isozyme analyses of allinase and G6PDH also showed a close relationship between ‘Mushhu–ninniku’ and leek. Isozymes of acid phosphatase (EC 3.1.3.2) and leucine aminopeptidase (EC 3.4.11.1) in ‘Mushhu–ninniku’ were also similar to those in leek (data not shown). Although, the size of allinase mRNA (1.9 kb) of ‘Mushhu–ninniku’ was identical to that of other *Allium* plants, its amount seemed to be less than the others. The N-terminal 25 amino acid sequence of ‘Mushhu–ninniku’ allinase was identical with that of leek, whereas that of the great-headed garlic allinase was distinctively different.

Thus, we conclude that ‘Mushhu–ninniku’, known as “Odorless Garlic” is a member of *A. ampeleoprasum* L., which has a close relationship to leek. Finally, if ‘Mushhu–ninniku’ is to be classified further, its nutritional and pharmacological properties and a more systematic study of its morphological characters will be required, because the species *A. ampeleoprasum* has many variations (Jones and Mann, 1963b).

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**Literature Cited**


無臭ニンニク’はAllium ampeloprasumに属する植物である

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摘要

天然無臭ニンニクといわれているネギ属植物について、植物学的、生化学的分析を行い、その種の同定を試みた。この植物は、正しい、鱗茎ともに通常のニンニクより大きく、鱗片は花茎に密着して鱗茎を形成する大型のものと、鱗茎の辺縁に付着する小型のものがあり、これらの数は20に及ぶ。花器はよく発達するが、ニンニクにみられる花序での特有な形状はない。染色体体は2n=32でリーグと同数であり、にんにくの2倍であった。そのDNAの制限断片長型(RFLP)は、リーグに似ており、ニンニク、エレファントガリックなどとは異なっていた。アイソサイム分析においてはリーグと最も似たパターンを示した。鱗茎細胞内でアリイナーゼ(C-Sリアーゼ)mRNAの発現は、他種に比べて少なく、大きさは等しく、1.9 kbであった。この植物のアリイナーゼのN末尾25アミノ酸残基の配列はリーグのそれと一致し、ニンニクとは2残基相違した。

以上の結果から、この植物は、リーグと極めて近縁の植物であり、Allium ampeloprasum L.の中に分類することができると考えられる。