Nuclear selection in monokaryotization of dikaryotic mycelia of *Pholiota nameko* as described by leading and following nuclei

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To examine monokaryotization of dikaryotic mycelia of *Pholiota nameko*, 18 monokaryotic stocks were used to produce a total of 130 dikaryotic stocks by reciprocal crossing. Monokaryotized mycelium was raised from dikaryotic mycelium in the peripheral zone of the growing colony. The stocks mated with a particular group of monokaryons produced wide-range monokaryotization at higher rates than the other combinations of hybridization. The growth rates of the monokaryotized mycelia exceeded from those of the corresponding parental dikaryons. The monokaryotized mycelium was isolated and back-crossed to parental monokaryotic stocks. Most of the isolates had nuclear types similar to only one of the parental stocks, while the replicates of isolates from two dikaryotic hybrids showed split nuclear type compositions. It is suggested that a relative dominance is active in the selection of one of the two nuclei of the dikaryotic cells in monokaryotization. The hierarchy of relative dominance among nuclei of 18 parental monokaryotic stocks in the monokaryotization of their reciprocal crossing products was estimated. We propose the involvement of a cascade process in dikaryotic cell division, in which the first dividing nucleus (to be found in the monokaryotized cell) may act as the "leading nucleus" and the other one as the "following nucleus."

Key Words——conjugate nuclear division; monokaryotization; nuclear selection; *Pholiota nameko*.

Pholiota nameko (Ito) Ito et Imai is an edible basidiomycetous fungus that forms fruit-bodies on the stumps or withered timbers of broad-leaved trees in both Japan and Taiwan from late autumn to spring (Imazeki, 1988). Due to the recent advances of bottle cultivation technology in Japan, this mushroom is now available in domestic markets throughout the year. However, the commercial spawns of this mushroom may have unstable genetic characteristics which lead to formation of monokaryotic hyphal cells from dikaryotic mycelia. This phenomenon can often lead to very poor production or a near total lack of fruiting when using inferior strains. Monokaryotization in the terminal hyphal cells of the developing colony was reported by Arita (1964, 1979). However, neither the genetic and molecular background for monokaryotization of this mushroom nor the mechanism of conjugate nuclear division in mushroom fungi have been reported.

Pholiota nameko has bipolar incompatibility factors (Arita and Takemaru, 1962). The bipolar factor system of *P. nameko* may make this fungus a more simplified experimental material than the tetrapolar mushrooms for the analysis of the function of incompatibility factors in hyphal conjugation in mushroom fungi. In this mushroom, monokaryotized mycelia can easily be isolated from the peripheral growing zone in a dikaryotic colony.

The hyphal monokaryotization is of great interest, since its probable cause is instability in the conjugate nuclear division, and it is expected to provide a clue in the analysis of the molecular control system involved in the conjugate nuclear division of basidiomycetes.

In the present study, we surveyed the manner of monokaryotization in the colonies of dikaryotic hybrid stocks produced by reciprocal crossing between various monokaryotic lines of stocks carrying different bipolar incompatibility factors in *P. nameko*. Further, we determined the nuclear type in the monokaryotized cells originating from dikaryotic hyphal cells, in order to demonstrate the relative dominance between the monokaryotized cell nucleus and the other parental nucleus in the formation of monokaryotic cells from dikaryotic hyphae of this fungus.

Materials and Methods

Organisms Various monokaryotic line stocks of *P. nameko* were obtained by single spore isolation from the fruit-bodies of various wild strains (Table 1). The incompatibility factors of the monokaryotic stocks were determined by crossing them against the tester stocks (NX-1 to NX-6) of known incompatibility factors (A1 to A6, respectively). The incompatibility factors of the stocks used for the present experiments were assigned tempora-

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Table 1.   Monokaryotic stocks of *Pholiota nameko*.

Stock No.	Incompatibility factor
NA-4	A1
NA-11	A1
NX-1	A1
NA-15	A2
NA-20	A2
NX-2	A2
NGW-9	A3
NGW-12	A3
NX-3	A3
NGW-19	A4
NGW-20	A4
NX-4	A4
NF-7	A5
NF-8	A5
NX-5	A5
NF-1	A6
NF-5	A6
NX-6	A6
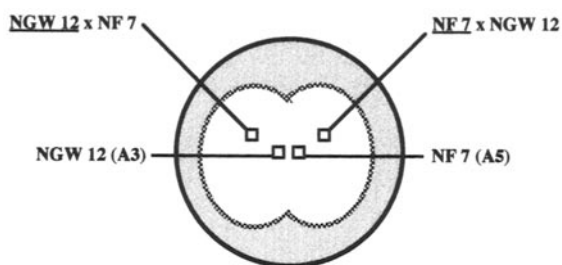
Fig. 1.   Isolation of dikaryotic hybrid mycelia in mating of *Pholiota nameko*.
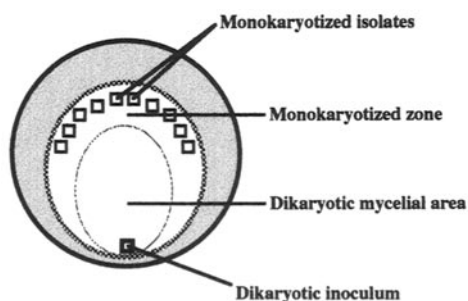
Fig. 2.   Isolation of monokaryotized mycelia from dikaryotic mycelial colony in *Pholiota nameko*.

ry numbers.

Culture conditions   Mycelial cultures were carried out in plastic Petri dishes (Iwaki, 90×15 mm) containing 12 ml of PDA medium (Nissui Pharmaceutical Co. Ltd.).   Plates were inoculated with a mycelial agar block (3×3×3 mm)

excised from the PDA stock slants of the test strain, and incubated at 20–22°C in a dark environment.

Method for mating   To obtain various mated stocks of this mushroom, monokaryotic stocks from each incompatibility factor group (e.g., A1) were mated to all other incompatibility factor groups (e.g., A2, A3, A4, A5 and A6), with three different stocks per group.   The mating inoculation was conducted by planting two different monokaryotic stocks 4 mm apart in the center of the PDA plate.   After incubating for about 2 weeks at 20°C in a dark environment, the mycelia having clamp connections were isolated from one site of the parental inocula as dikaryotic hybrids having one parental cytoplasmic characteristic (Fig. 1).

Determination of monokaryotized mycelial zone in hybrid colonies   The hybrid stock mated using the above method was inoculated 6 mm from the site of the dish to allow for extended hyphal growth.   After 9–12 days of cultivation, the mycelial colony was dissected into 1-mm sections, from the terminal edge to the inoculum point, and each section was microscopically examined for the absence of hock cells.   The length from the peripheral monokaryotic section to the border of the inner heterokaryotic area was determined as the area of hybrid monokaryotization for the test dikaryon.   Five replicates were applied for each of the test hybrid stocks.

Determination of terminal cell incompatibility factors   Ten replicates of mycelial pieces from each mated hybrid stock were isolated from different portions in the monokaryotized zone of the dikaryotic colony grown on the PDA plate (Fig. 2).   They were cultured on PDA slants.   These monokaryotic isolates were then back-crossed to both of the respective parental monokaryotic stocks.   The parental strain that showed incompatibility with the test mycelium was identified with the nucleus of the parental strain from which the nucleus of monokaryotized mycelium originated.

Results

Various patterns of colony growth in dikaryotic hybrid stocks of *P. nameko*   The dikaryotic hybrid stocks of *P. nameko* showed several different types of colony growth patterns on the PDA plates.   Figure 3a shows a typical morphology of the colony, which formed a thick uniform aerial mycelium surrounded by low density aerial mycelium in the peripheral zone.   The isolated mycelia from the outer zone of the dikaryotic colony usually showed monokaryotic characteristics with no hock cells.   In Fig. 3b, a sector was formed at the left side of the colony.   In Fig. 3c, irregular density portions of mycelia were formed in the inner heterokaryotic area of the colony.   Fig. 3d shows the zonation of colony growth, where the accumulation of yellowish pigment in radial growth and a faint outer growth zone were observed.   It is probable that hyphal conjugation between an original dikaryotic cell and a monokaryotized cell might produce the irregular appearance of colonies in this mushroom.

Estimation of monokaryotized outer hyphal zone in the growing colonies of various dikaryotic hybrid stocks   Ta-

(a) NX-1 x NA-20

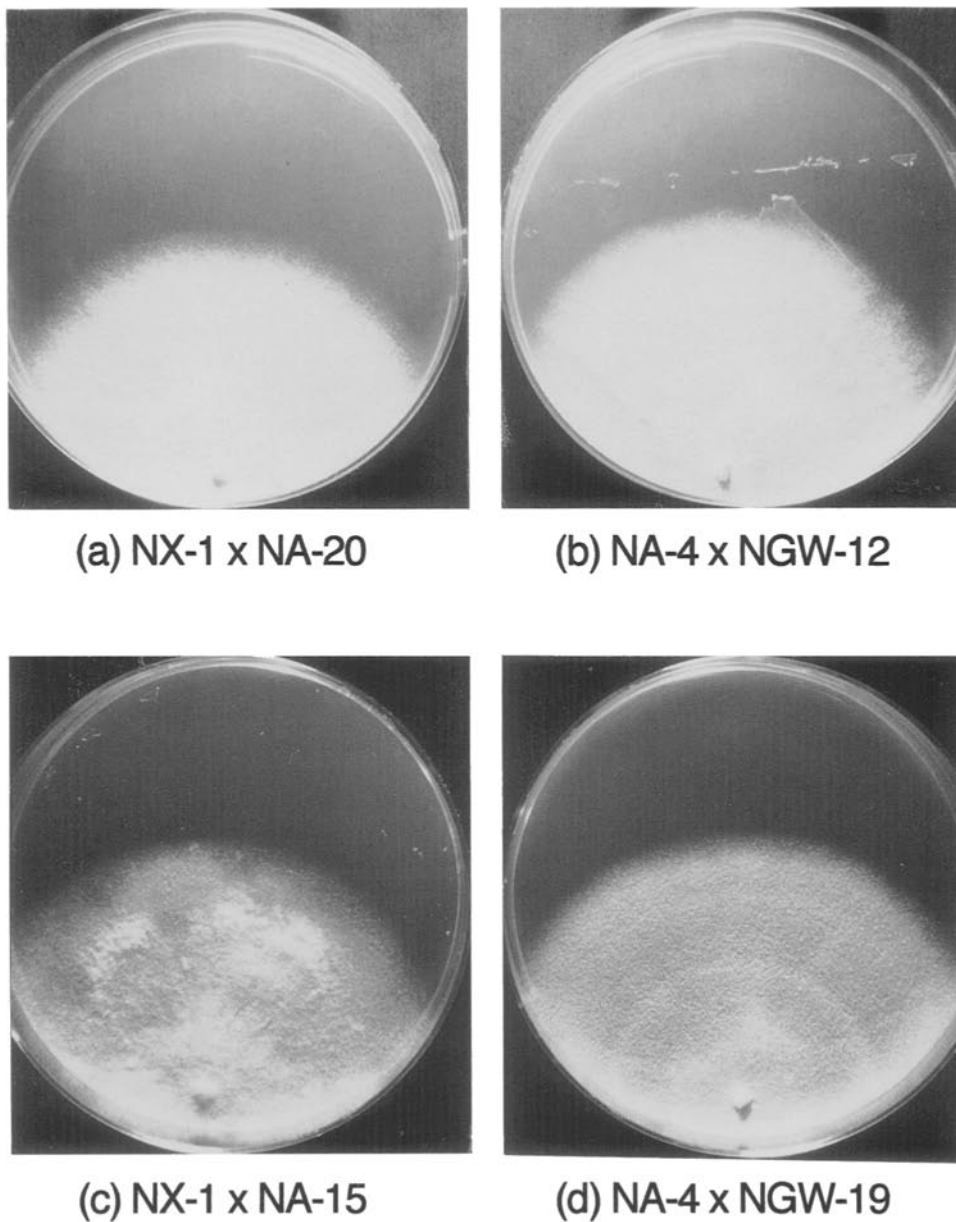(b) NA-4 x NGW-12

(c) NX-1 x NA-15

(d) NA-4 x NGW-19

Fig. 3. Different colony appearances in various dikaryotic hybrid stocks of *Pholiota nameko*. (a) A typical dikaryotic colony, which grew to form thick uniform aerial mycelium in the inner area and produced low density aerial mycelium in the peripheral zone. (b) Formation of sector at the left side of the colony. (c) Formation of irregular density portions of mycelia within the colony. (d) Zonation in colony growth.

ble 2 shows the different widths of monokaryotized peripheral zones of the colonies determined for the 130 mated dikaryotic stocks. The colonies of some hybrid stocks (underlined at upper left in Table 2) produced a wide area of monokaryotization stretching from 15 to 19 mm from the colony margin. It appears that the mated stocks with a special group of monokaryons, such as NA-15 and NGW-12, produced the wide-range monokaryotization at higher rates than other combinations. Besides, in the stocks underlined at lower right in Table 2, monokaryotic areas were less than 1 mm in width. Furthermore, the mating with NGW-9 monokaryon seems to produce mostly stable heterokaryotic growers. Differences in the ability of one nucleus to lead the conjugate division with another nucleus in dikaryotic cells of the hybrid colony might result in differences in the instability which causes monokaryotization.

The faster growth characteristic of monokaryotized mycelia Arita (1968) reported that monokaryotic mycelia of his test stocks showed more rapid growth than the dikaryons. We also supposed that the variable width of the monokaryotized zone in the growing colony of dikaryotic stocks might be the result of different growth rates of the monokaryotized mycelia from the parental

Table 2. The width of monokaryotized terminal mycelial zones and the ratio of monokaryotic mycelial zones in dikaryotic mycelial colonies of various hybrid stocks in *Pholiota nameko*.

Mated stock	Mono. width (mm)	Ratio of monokaryotic width[a]	Mated stock	Mono. width (mm)	Ratio of monokaryotic width[a]	Mated stock	Mono. width (mm)	Ratio of monokaryotic width[a]
NA-4×NF-5	18	0.39	NA-11×NF-7	6	0.12	NX-3×NF-5	3	0.05
NA-15×NGW-12	18	0.38	NX-2×NX-6	8	0.12	NX-1×NX-6	3	0.05
NGW-20×NF-8	18	0.38	NX-1×NA-20	6	0.12	NX-1×NGW-9	3	0.05
NGW-12×NX-4	19	0.37	NX-1×NGW-12	6	0.11	NA-11×NGW-9	3	0.05
NGW-12×NGW-19	18	0.36	NA-15×NF-8	6	0.10	NX-2×NF-7	3	0.05
NX-1×NX-2	18	0.35	NA-20×NX-5	6	0.09	NGW-12×NF-8	3	0.05
NA-20×NGW-12	18	0.35	NA-20×NF-1	6	0.09	NX-3×NGW-20	3	0.05
NA-4×NX-2	19	0.34	NF-7×NX-6	5	0.09	NGW-12×NF-7	3	0.05
NA-11×NGW-20	15	0.33	NX-3×NX-5	5	0.09	NA-20×NF-7	3	0.05
NGW-20×NF-5	18	0.33	NA-4×NGW-12	5	0.09	NA-11×NGW-12	3	0.05
NA-15×NX-4	15	0.33	NX-1×NF-7	5	0.09	NX-2×NX-4	3	0.04
NX-2×NGW-19	18	0.32	NA-20×NGW-9	5	0.09	NX-4×NF-5	3	0.04
NA-15×NGW-20	15	0.31	X-1×NX-3	5	0.09	NF-7×NF-1	3	0.04
NA-15×NX-3	19	0.30	GW-19×NX-5	5	0.09	NGW-19×NF-8	3	0.04
NA-11×NX-5	13	0.27	NA-11×NX-3	6	0.08	NA-15×NX-6	3	0.04
NA-11×NF-8	13	0.26	NA-20×NF-8	6	0.08	NA-11×NX-6	2	0.04
NX-5×NF-5	15	0.25	NA-4×NX-6	6	0.08	NX-5×NF-1	2	0.04
NA-4×NA-20	17	0.24	NX-3×NF-1	5	0.08	NX-1×NF-5	2	0.04
NA-4×NA-15	15	0.24	NX-1×NA-15	5	0.08	NF-8×NF-5	2	0.03
NA-15×NX-5	13	0.24	NGW-12×NX-6	5	0.08	NA-20×NX-6	2	0.03
NGW-20×NX-5	13	0.23	NX-3×NGW-19	5	0.08	NF-7×NF-5	2	0.03
NX-3×NF-8	12	0.20	NA-15×NF-1	4	0.08	NX-5×NX-6	2	0.03
NA-15×NF-5	11	0.20	NA-4×NGW-9	4	0.08	NA-15×NGW-19	1	0.02
NA-11×NF-5	11	0.20	NA-11×NGW-19	5	0.08	NGW-9×NF-1	1	0.02
NGW-20×NF-7	10	0.19	NA-20×NX-3	5	0.07	NF-8×NF-1	1	0.02
NA-4×NF-1	11	0.18	NF-8×NX-6	5	0.07	NX-4×NF-8	1	0.02
NX-1×NX-5	10	0.17	NX-2×NGW-12	4	0.07	NX-4×NX-5	1	0.01
NGW-12×NF-5	10	0.17	NA-15×NGW-9	4	0.07	NGW-19×NX-6	1	0.01
NX-1×NF-8	10	0.17	NX-1×NX-4	4	0.07	NX-2×NGW-9	<1	—
NA-4×NGW-19	10	0.17	NX-2×NX-5	4	0.07	NX-2×NGW-20	<1	—
NGW-12×NX-5	9	0.16	NX-1×NGW-19	4	0.07	NX-2×NF-5	<1	—
NGW-20×NX-6	8	0.16	NX-2×NX-3	4	0.07	NGW-9×NF-7	<1	—
NX-2×NF-8	10	0.15	NX-2×NF-1	4	0.07	NGW-9×NF-8	<1	—
NGW-9×NX-4	8	0.15	NA-20×NGW-20	4	0.07	NGW-9×NX-5	<1	—
NX-1×NGW-20	8	0.15	NA-20×NX-4	4	0.07	NGW-9×NF-5	<1	—
NA-15×NF-7	8	0.15	NA-4×NX-3	4	0.07	NGW-9×NX-6	<1	—
NA-11×NX-4	7	0.15	NA-4×NX-4	4	0.07	NGW-12×NF-1	<1	—
NGW-9×NGW-19	12	0.14	NX-3×NX-4	4	0.07	NX-3×NF-7	<1	—
NGW-12×NF-7	11	0.14	NA-20×NGW-19	4	0.07	NX-3×NX-6	<1	—
NGW-9×NGW-20	6	0.14	NA-4×NX-5	4	0.06	NGW-19×NF-1	<1	—
NGW-12×NGW-20	8	0.13	NA-11×NA-15	4	0.06	NGW-19×NF-5	<1	—
NA-4×NGW-20	8	0.13	NA-20×NF-5	4	0.06	NGW-20×NF-1	<1	—
NA-11×NA-20	8	0.12	NA-11×NX-2	3	0.05	NX-4×NF-7	<1	—
						NX-4×NF-1	<1	—

a) The monokaryotic width percentages were determined by dividing the monokayotic width by total hypal growth of colonies.

dikaryotic mycelia. To confirm this supposition, the growth rates of several monokaryotized isolates and their parental dikaryotic stocks were compared. The results are shown in Table 3.

Table 3.   Comparison of the growth rates of dikaryotic mycelia and their monokaryotized mycelia in *Pholiota nameko*.

Mated stock (Dikaryon)	Growth rate (mm/day)	
	Dikaryotic mycelium	Monokaryotized mycelium
NX-2 × NX-1	11	15
NX-3 × NX-2	12	15
NX-3 × NX-4	12	13
NX-5 × NX-4	11	19
NX-2 × NX-5	14	19

The test stocks of dikaryotic hybrid mycelia showed different growth rates from each other, and the growth rates of the monokaryotized mycelia exceeded those of the corresponding parental dikaryons. Therefore, once monokaryotized cells were formed in the terminal hyphal growing zone of the dikaryotic colony, the outer monokaryotized mycelial area was enlarged by the colony development.

Selection of nucleus in the monokaryotization from dikaryotic hyphal cells of the mated stocks In 1964, Arita observed the selection of nuclear types in monokaryotization by using several mated products. He reported that both parental nuclear types of monokaryotic mycelia were isolated, although one type was recovered at a high rate (67-83%) in the monokaryotized cells from the dikaryotic parents. We attempted to determine which parental nucleus predominated in the monokaryotized cells of 34 dikaryotic hybrid stocks. In these experiments, the incompatibility factors were used as nuclear markers to identify the parental nuclei involved in the dikaryotic cells. The results are shown in Table 4.

Except for those from two dikaryotic hybrids, all of the monokaryotized isolates had nuclear types similar to only one of the parental stocks. The replicates of monokaryotic isolates from two dikaryotic hybrids showed split incompatibility factor compositions. In the cross of NX-1 × NX-6, 70% of the monokaryotic isolates were A1 factored, and the remainder were A6 factored. In case of the hybrid of NX-3 × NF-5, 40% were A3 factored, while 60% were A6 factored.

Relative dominance of the monokaryotized cell nucleus over the other parental nucleus in the monokaryotization of various dikaryotic stocks Table 4 also suggests that a relative dominance is active in the selection of one of the two nuclei of the dikaryotic cells in monokaryotization. In the case of NA-4 × NA-20 hybrids, only the NA-4 nucleus was found in the monokaryotized cells, but the same nucleus was recessive with respect to the NX-3 nucleus in the monokaryotization from the NA-4 × NX-3. The hierarchy of relative dominance among nuclei of 18

parental monokaryotic stocks in the monokaryotization of their reciprocal crossing products was estimated and summarized in Fig. 4. This figure involves a partial discrepancy in two specific nuclear compositions of hybrid dikaryons: at the top of the figure, NX-3 monokaryons consistently yielded A3 incompatibility factor monokaryotized cells when mated with all of the strains below, with the exception of NX-5 and NF-5 (see Table 4).

Discussion

The formation of monokaryotized cells from dikaryotic mycelia of basidiomycetes has been reported in *Typhula trifolii* Postr. (Nobles, 1937), *Polyporus pseudoboletus* Speg. (Furtado, 1966), *Coprinus disseminatus* (Fr.) S. F. Gray (Butler, 1972), and *Armillariella mellea* (Fr.) Karst (Korhonen and Hintikka, 1974). These authors suggested that the hyphal monokaryotization was caused by the sorting out of the nuclei into uninucleate hyphal segments or branches. On the other hand, Arita (1979) proposed a different mechanism for the monokaryotization in *P. nameko*. He supposed that one member of a conjugate pair of nuclei in the dikaryotic terminal and the subterminal segments underwent repeated independent divisions. Then the cells containing the homokaryotic nuclei are delimited from the heterokaryotic multinucleate cells by the formation of one or more septa, and the resulting monokaryotized cells develop into monokaryotic hyphae.

The estimation of the monokaryotized outer hyphal zone in the growing colonies demonstrated that zones of different widths were produced by various mated stocks. It appears that the mated stocks with a particular group of monokaryons produced higher monokaryotic width percentages than the average of all stocks tested. In addition, mating with another type of monokaryons seemed to produce stable heterokaryotic growers. It is assumed that the two nuclei of dikaryotic cells might not contribute equally to the total expression of the stability of the dikaryotic condition in the mated stocks.

The monokaryotization of dikaryotic mycelium of *P. nameko* involves a process of nuclear selection. Arita (1979) reported that both parental nuclear types of monokaryons were isolated, although one type was predominant in the monokaryotized cells from the dikaryotic parents. We observed that all the monokaryotized isolates except for those from two dikaryotic hybrids had the same nuclear types, derived from only one of the parental stocks. These results illustrate that one nucleus which is predominant in the monokaryotization of a dikaryotic stock may generally act as either dominant or recessive in a different combination of hybrid dikaryons. The hierarchy of the nuclei of 18 parental monokaryotic stocks in the monokaryotization of their reciprocal crossing products was estimated by comparing the relative dominance among them. Although a partial discrepancy between two specific nuclear composition of hybrid dikaryons is involved, the rule of relative dominance seems to be active in the selection of the nucleus for monokaryotized cell formation from dikaryo-

Table 4. Analysis of nuclear types of the monokaryotized isolates from various hybrid dikaryotic mycelia in *Pholiota nameko*.

Mated stock	Predominant nuclear type of monokaryotized isolates[a]		Mated stock	Predominant nuclear type of monokaryotized isolates[b]	
NA-15×NX-3	NX-3	(10/10)[b]	NX-2×NGW-12	NGW-12	(10/10)
NA-4×NX-3	NX-3	(10/10)			
NX-1×NX-3	NX-3		NGW-19×NX-5	NGW-19	
NX-3×NGW-19	NX-3		NGW-19×NF-7	NGW-19	
NX-3×NF-5	NF-5	(6/10)	NGW-19×NF-8	NGW-19	
NX-3×NX-5	NX-5	(10/10)	NA-20×NGW-19	NGW-19	
NA-20×NX-3	NX-3		NGW-9×NGW-19	NGW-19	
NA-11×NX-3	NX-3				
NX-3×NF-1	NX-3		NX-5×NF-5	NX-5	
NX-2×NX-3	NX-3		NX-5×NX-6	NX-5	(10/10)
NX-3×NGW-20	NX-3		NA-20×NX-5	NX-5	
			NX-5×NF-1	NX-5	(10/10)
NA-4×NA15	NA-15	(10/10)	NX-4×NX-5	NX-5	(10/10)
NA-15×NGW-12	NA-15	(10/10)	NX-2×NX-5	NX-5	
NA-15×NX-5	NA-15		NGW-20×NX-5	NX-5	(10/10)
NA-15×NF-5	NA-15				
NA-15×NF-7	NA-15	(10/10)	NF-7×NF-5	NF-5	
NA-15×NX-6	NA-15	(10/10)	NF-8×NF-5	NF-5	
NA-11×NA-15	NA-15		NA-20×NF-5	NF-5	
NA-15×NX-4	NA-15		NX-4×NF-5	NF-5	(10/10)
NA-15×NGW-20	NA-15	(10/10)	NGW-20×NF-5	NF-5	(10/10)
NA-4×NGW-12	NA-4	(10/10)	NF-7×NX-6	NF-7	
NA-4×NGW-19	NA-4		NA-20×NF-7	NF-7	
NA-4×NF-5	NA-4		NF-7×NF-1	NF-7	
NA-4×NX-6	NA-4				
NA-4×NA-20	NA-4	(10/10)	NF-8×NX-6	NF-8	
NA-4×NF-1	NA-4	(10/10)	NA-20×NF-8	NF-8	(10/10)
NA-4×NX-4	NA-4		NF-8×NF-1	NF-8	
NA-4×NX-2	NA-4				
NA-4×NGW-20	NA-4	(10/10)	NA-20×NX-6	NX-6	
NA-4×NGW-9	NA-4		NX-2×NX-6	NX-6	
NX-1×NGW-12	NX-1		NA-11×NA-20	NA-20	
NX-1×NGW-19	NX-1		NA-20×NX-4	NA-20	
NX-1×NX-5	NX-1	(10/10)	NA-20×NF-1	NA-20	(10/10)
NX-1×NF-5	NX-1	(10/10)	NA-20×NGW-9	NA-20	
NX-1×NF-7	NX-1	(10/10)	NA-20×NGW-20	NA-20	(10/10)
NX-1×NF-8	NX-1				
NX-1×NX-6	NX-1	(7/10)	NA-11×NF-1	NA-11	
NX-1×NA-20	NX-1		NA-11×NX-2	NA-11	
NX-1×NX-4	NX-1		NA-11×NGW-9	NA-11	
			NX-1×NX-2	NX-1	
NX-1×NGW-20	NX-1	(10/10)	NF-1×NX-4	NF-1	
			NX-2×NF-1	NF-1	
NGW-12×NGW-19	NGW-12	(10/10)			
NGW-12×NF-5	NGW-12	(10/10)	NX-2×NX-4	NX-4	
NGW-12×NF-7	NGW-12	(10/10)	NGW-9×NX-4	NX-4	(10/10)
NGW-12×NF-8	NGW-12	(10/10)			
NA-20×NGW-12	NGW-12		NX-2×NGW-20	NX-2	
NA-11×NGW-12	NGW-12				
NGW-12×NX-4	NGW-12		NGW-9×NGW-20	NGW-20	

a) Three isolates from each hybrid dikaryon were examined for their nuclear type(s).
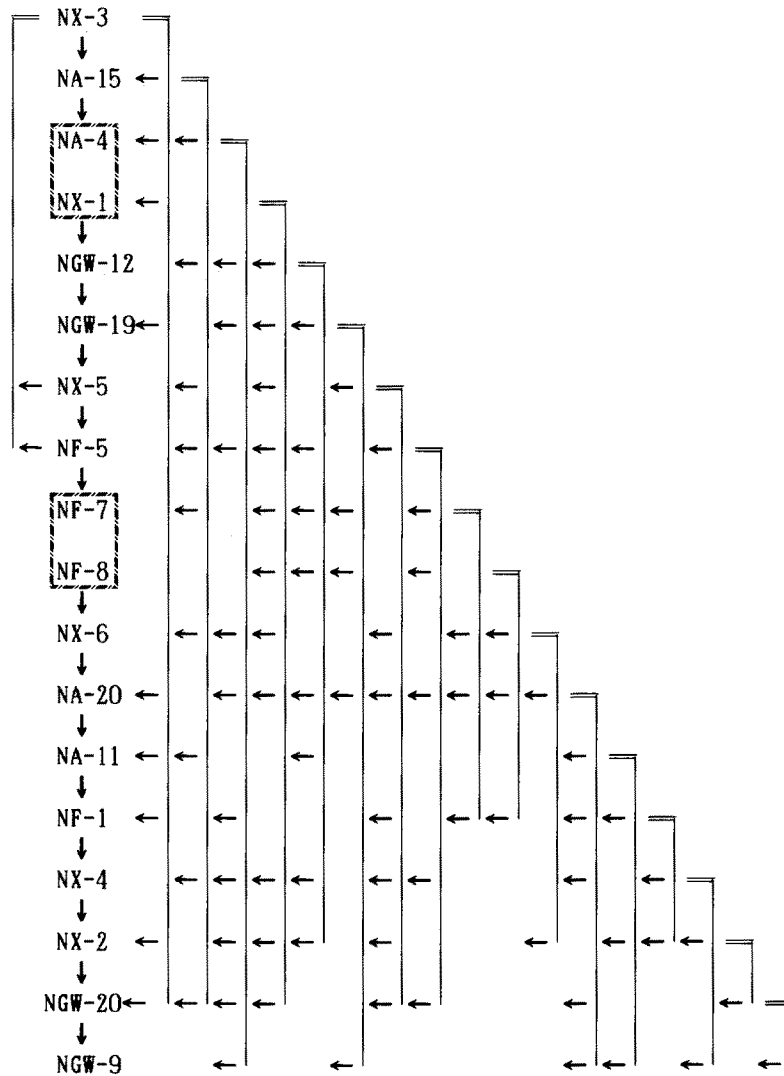b) The hybrid monokaryons in parentheses were tested using ten isolates.

Fig. 4. Hierarchy of relative predominance among 18 parental monokaryotic stocks in the monokaryotization of their reciprocal crossing products in *Pholiota nameko*.

tic hyphae.

While it is currently accepted that both nuclei divide in unison in the conjugate cell division of dikaryotic mycelium, we suspect that the actual nuclear division might be cascaded. In this operational hypothesis, one nucleus in the dikaryotic cell might divide slightly earlier than the other, and the first dividing nucleus (which will be found in the monokaryotized cell) may act as the "leading nucleus," and the second one may divide under the control of the former as a "following nucleus." Inferior control in this system may cause the monokaryotization of dikaryotic cells. Since the monokaryon possessing the leading nucleus consistently persists in monokaryotization, it may be possible that the leading-nucleus monokaryon also genetically contributes other traits that dominate expression of the following nucleus monokaryon in breeding. Furthermore, the unique system of monokaryotization in *P. nameko* may potentially be used to analyze the mechanism of conjugate nuclear division.

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