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A New Index "Node Order" and the Distinction of Sections of the Genus *Sasa*

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新しい指数節序とそれを用いたササ属節の区分

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A new index "Node Order" is a numbered order of nodes on a culm of dwarf bamboo. The lower node of the longest internode is designated as "0" (NDO 0). Nodes at higher levels than this one are referred to as +1, +2, +3 .... etc. to the top; nodes lower than "0" are –1, –2, –3 .... as they approach the base. This node order is available to distinguish 3 sections of *Sasa,* Crassinodi, Macrochlamys, and Sasa. By using this index in combination with ANOHCB and RHHCB, which are other indexes proposed by the authors, it is proved to be more effective in the distinction of these three sections even under disturbed conditions.

Considerable attention has been paid to the genus *Sasa* because it is widespread in Japan and because its morphological variability in relation to environmental conditions is not always clear. Although many morphological species have been published (Makino and Shibata 1901, Nakai 1931, 1933–1935, 1934–1936, etc., Koidzumi 1934–1943, etc., Tatewaki 1940, etc.), they were defined by herbarium materials not by living specimens of populations (Usui 1961, Suzuki S. 1961 and 1962). Thus, it is often difficult to identify *Sasa* plants in ecologically different spots. On the other hand, a contrasting distributional differentiation of *Sasa,* sect. Macrochlamys and Crassinodi, has been recognized in the mainland Japan (Yamazaki 1959). It is represented by the Crassinodi Line correspond to the dorsiventrality of vegetation associated with the climatic difference (Suzuki S. 1961, Usui 1961 and 1972, Suzuki H. 1962, Suzuki T. 1963 and 1967, etc.).

Sections of *Sasa* defined mainly by the branching type of culms are readily recognizable in the field. Thus, Usui (1961) insisted that the species conception of this genus should be based on living populations, and his species deduced from living populations were nearly equal to the sections set forth by Nakai (1931 and 1934) in size and involvement of variations.

In the classification of *Sasa,* it is the starting point to define the section to which the *Sasa* plant

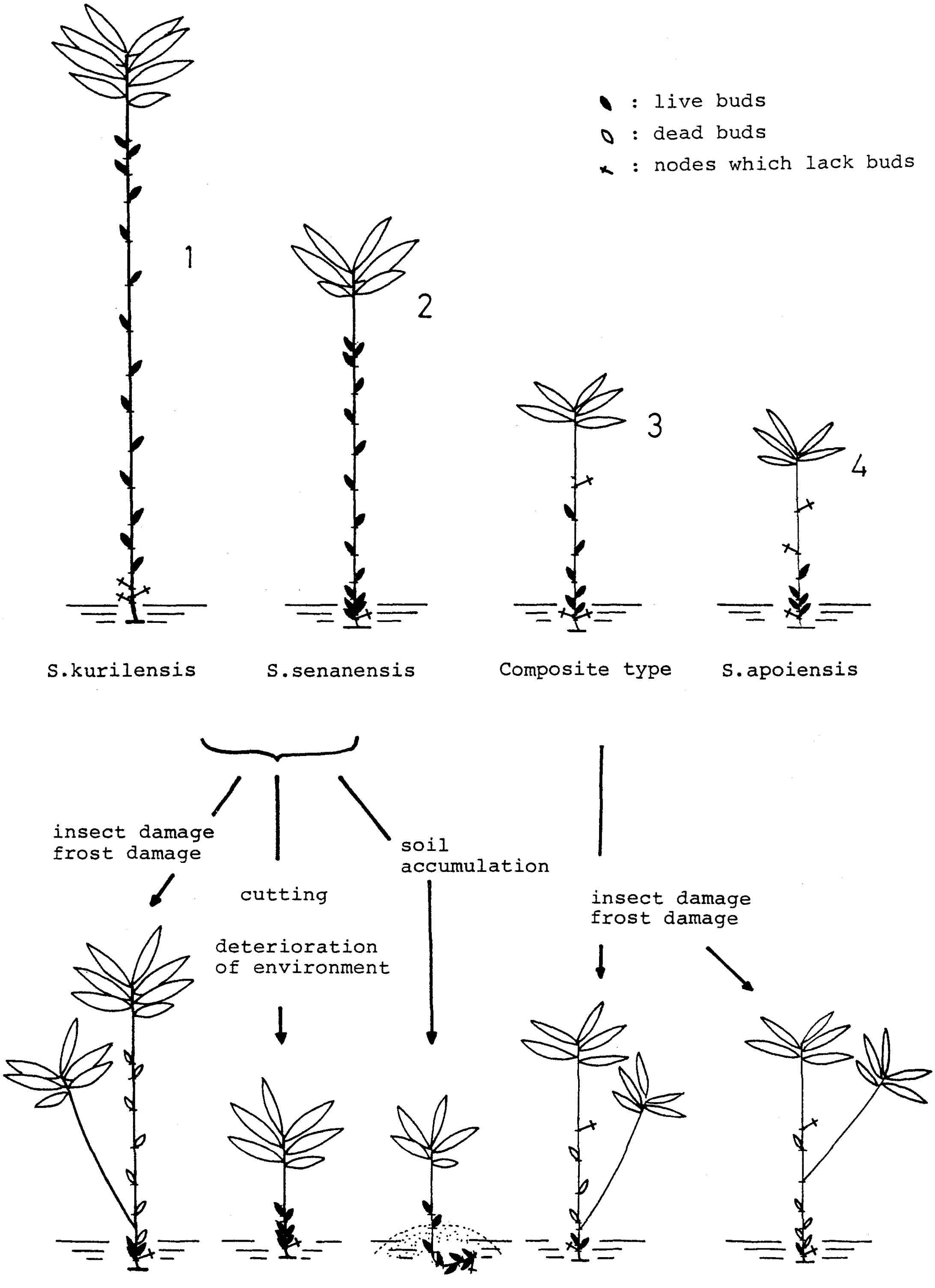

Fig. 1. Modification of buds in position and vitality by some biotic and abiotic factors. Species represent 3 sections of *Sasa*. *S. kurilensis*: sect. Macrochlamys; *S. senanensis*: sect. *Sasa*; Composite type: an intermediate type of Sasa between sect. *Sasa* and sect. *Crassinodi; S. apoiensis:* sect. *Crassinodi.*

under question belongs. For this purpose we paid our attention to the bud position of *Sasa,* because the arrangement of buds on culms is closely associated with the branching type. The 'branching type' in this paper is schematic rather than the actual; branchings are easily modified by environmental influence such as frost damage, insect damage, etc. (Fig. 1).

In the previous paper (Niiyama and Ito 1983), we recognized 3 types, S(=E) type, Cr type and Co type, in relation to 2 sections of the genus *Sasa,* Sasa and Crassinodi, in Hokkaido by using the "RHHCB" (Relative Height of the Highest Culm Bud), which indicates the highest position of bud attachment on a culm. This specified position showing the arrangement variations of latent buds is statistically and significantly stable in discriminating three types mentioned above (Fig. 2).

It is most important to define the standard position of buds on the culms to secure reliable comparative investigation of bud arrangement. Usually, bud position is represented by node number counted from the ground level. However, the ground level is differently recognized by different investigators and in different occasions. To avoid this inaccuracy and instability in counting, we designed a new index "Node Order" (NDO) in relation to the longest internode of a culm.

In this paper, we attempt to test the effectiveness of NDO discriminating the three types mentioned previously based on living assemblages of *Sasa.*

Materials and Methods

Materials are individual culms selected from members of the three types of *Sasa* and the forth type or M type, represented by *Sasa kurilensis* Makino et Shibata, a representative of the section Macrochlamys. Twenty quadrats belonging to S, Cr and Co type were chosen along an environmental gradient in the central and the eastern parts of Hokkaido as shown in Fig. 3. Four sample plots were selected additionally in the extra-routes. Five sample plots of M type were set sporadically. On

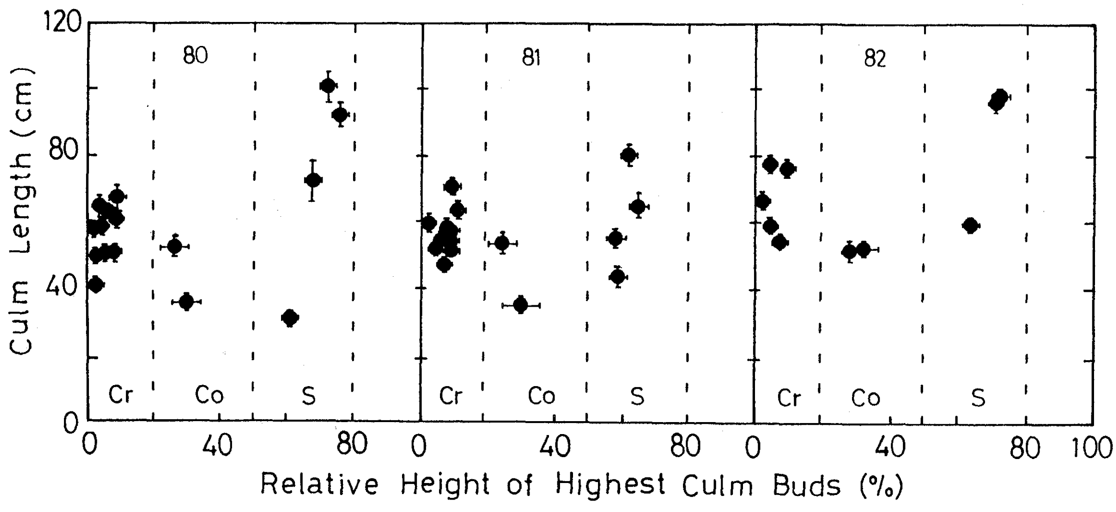

Fig. 2. The relation between culm length of *Sasa* and the highest position of culm buds (in % to the total culm length). The figure shows the constancy of the highest position of culm buds in 3 years' observation from 1980 to 1982 in each type. 80:1980; 81:1981; 82:1982. Cr: Crassinodi type; Co: Composite type; S: Sasa type. (vertical and horizontal bars show 80% conf. intervals).

each quadrat, emergence and fall of buds were observed, and 20 to 240 culms were collected in each quadrat between 1980 and 1983.

All culms collected were current shoots and found to be independent above the ground. The length of internodes, and performance of buds on culms were recorded in all samples.

Terminology

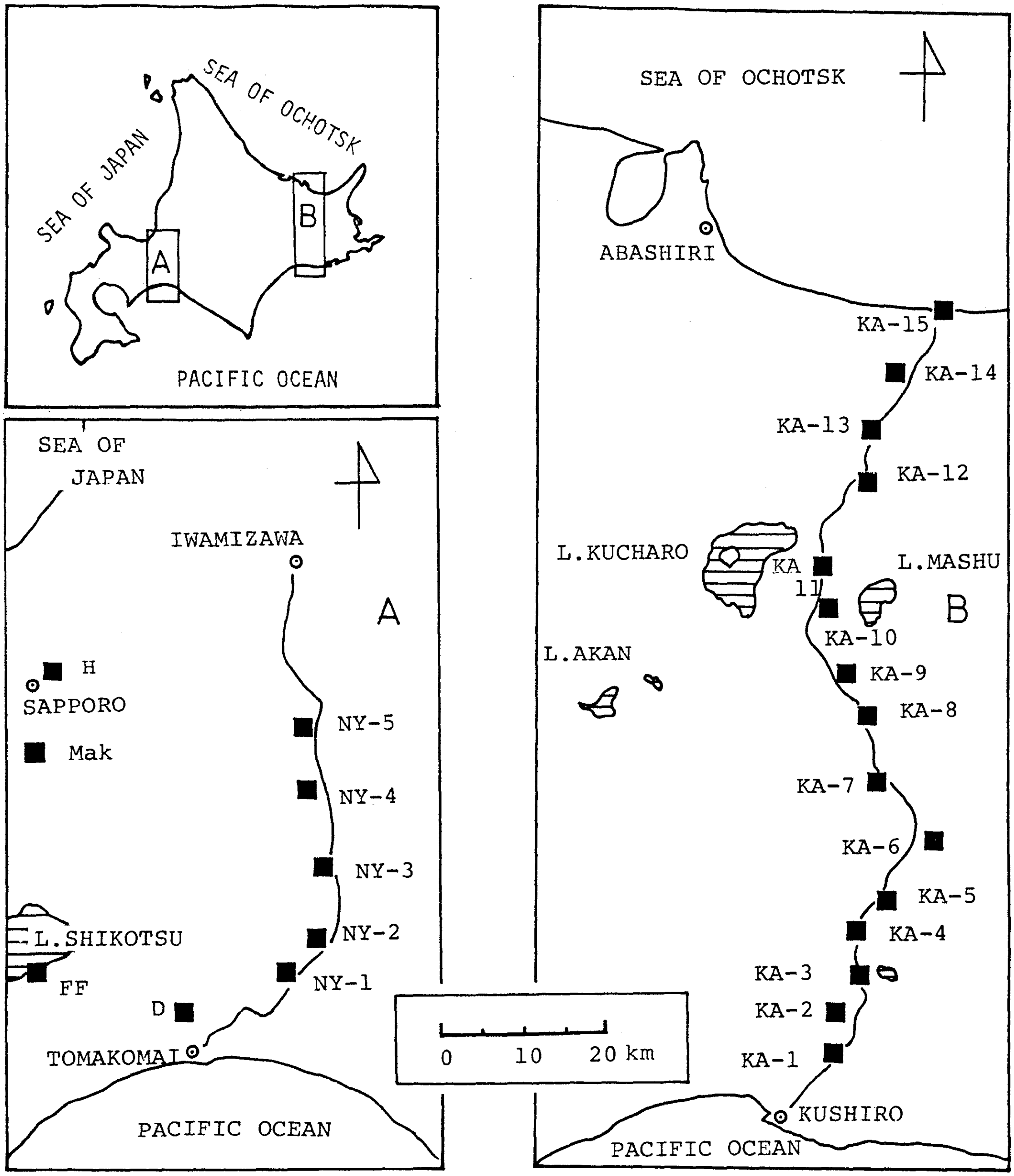

Fig. 3. Sample plots and quadrats along Route A (left) and B (right), and additional quadrats (D, FF, H, and Mak). D: Tomakomai Experimental Forest Fac. Agr. Hokkaido Univ.; FF: a place at the foot of Mt. Fuppushi; H: Campus of Hokkaido Univ.; Mak: Makomanai in Sapporo City. Plot names on the routes are omitted.

(1) RHHCB (Relative Height of the Highest Culm Bud):

$$\frac{\text{The highest attachment position of buds on a culm from the ground surface (cm)}}{\text{Total length of a culm (cm)}} \times 100\ (\%)$$

(Niimiya and Ito 1983)

(2) NDO (Node Order): This is a numbered order of nodes on a culm. The lower node of the longest internode is designed as "0" (NDO 0). Nodes which at higher positions from this "0" are referred to as +1, +2, +3 ...... to the top; nodes lower than the "0" are –1, –2, –3 ...... as they approach the base. This is shown in Figure 4.

(3) ANOHCB (Average Values of NDO of the Highest Culm Bud): Average values of NDO which is represented by the range of the highest attachment position of the bud.

(4) Cr type (Crassinodi type): A type characterized by a few branches from the lower part of culm, in which RHHCB ranges from 0 to 20% (Niimiya and Ito 1983).

(5) S type (Sasa type): A type characterized by scattered branches from the base to the top of culms, in which RHHCB ranged from 50 to 80%. (Niimiya and Ito 1983).

(6) Co type (Composite type): A type characterized by branches in which RHHCB ranges from 20 to 50%. (Niimiya and Ito 1983).

Results

1. Node Order The length of internodes on a culm increases generally from the base toward the top. But the increase ceases at a part of the culm and then turns to decrease. This is a common feature in all *Sasa* plants. From this fact the longest internode is chosen as a standard of the determination of the bud position of the culm. The regularity of the increase and the decrease of the internode length is shown in Figure 5. As seen in Figure 5, normalized internode length curves show a common feature in Cr, Co and S types except for M type (*S. kurilensis*). It revealed in the former three types that a decrease in the internode length was sharper in the upper internodes (+ side) from the longest internode than in the lower one (– side). However, the curves were nearly symmetrical. In M type the curve was different from those of the former and rather skewed in outline; in the upper internodes, a decrease of the length was gradual as compared with that in the lower ones.

The range of latent bud position on the culm was measured by the NDO, and four types were distinguished. Type 1: buds are limited to "–" values of the NDO. Type 2: buds range from near "0" to "–" values. Type 3: buds range from "–" to "+" values. And type 4: from "–" to "+" but mainly in "+".

Results are summarized as follows: the first three types based on the NDO are in agreement with the three types classified by the RHHCB in the previous paper (Niimiya and Ito 1983); type 1 corresponds to Cr type; type 2 to Co type; type 3 to S type; and type 4 to M type or *S. kurilensis*.

2. The relation of the RHHCB to the ANOHCB The RHHCB and ANOHCB were measured in 25 plots during 3 years from 1980 to 1982 as seen in Figure 6. From this it was shown that the NDO values were stable and worked as a key in comparison of different types of *Sasa*. It was clear that the ANOHCB was correlated to the RHHCB. Cr type corresponded to the NDO range from –1 to 13; S type from +1 to +3; and Co type from –1.5 to +1.5. In M type it was more than +8. Section Macrochlamys was not necessarily distinguished from S type in the field by the RHHCB alone, because the RHHCB of larger plants of S type was closer to the smaller M. However, when the ANOHCB was used together

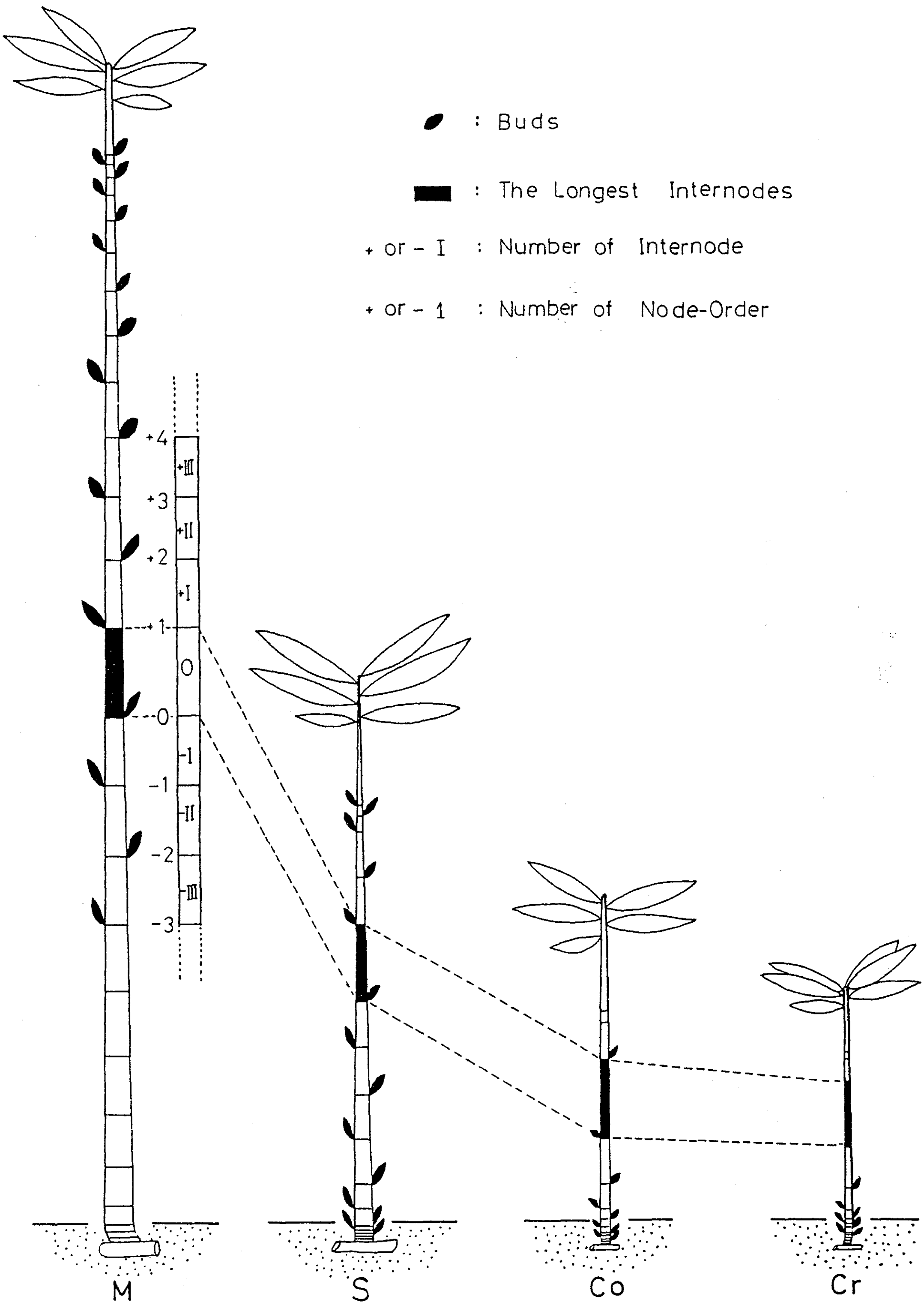

Fig. 4. Node Order, that is, a node number on the culm of *Sasa*. Arabic numeral: the node number; Roman numeral: the internode number.

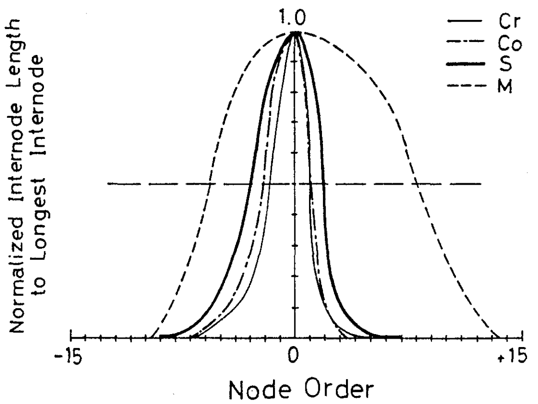

Fig. 5. Curves show the regularity of the relation between normalized internode length and the longest internode length. Broken line: 50% level of normalized internode length. Cr, Co and S see Fig. 2. M: Macrochlamys type.

with it, the difference between S type and M type was more clear cut. From the facts mentioned above the ANOHCB was available to distinguish the both types in association with the RHHCB, and it was suggested that the position and the range of buds on the culm were governed by genetical factors, although the phenotypic pattern of emergence of buds was somewhat modified by environmental influences.

3. Emergent pattern of latent buds Buds of *Sasa* are formed on the current shoots as latent buds by the summer season, and there are four types of buds. (1) The winter bud: the bud begins to enlarge on the current shoots in the autumn and complete the branching in the next autumn. (2) The spring bud I: the bud remains as the latent bud in the winter and begins to enlarge in the following spring. The completion of the branching is in autumn. (3) The spring bud II: the bud remains as the latent bud during the winter and begins to enlarge in the following spring. The completion of the branching is in the following autumn. And (4) the spoiled bud: the bud appears as the latent bud but usually becomes inactivate, not enlarging.

Figure 7 shows three consecutive year changes of the frequencies of the three types of buds from 1980 to 1982. As seen in Figure 7, in S type the latent bud distributed from –5 to +5 in the NDO. In the first year the winter bud appeared from –2 to +4, but most of them appeared between 0 and +2. In the second year the winter bud increased on both upper and lower parts of culms than those in the first year. They appeared from –4 to 0 and from +3 to +4. In the third year the winter bud appeared in the lower parts, from –5 to –1. The spring bud (the spring bud I

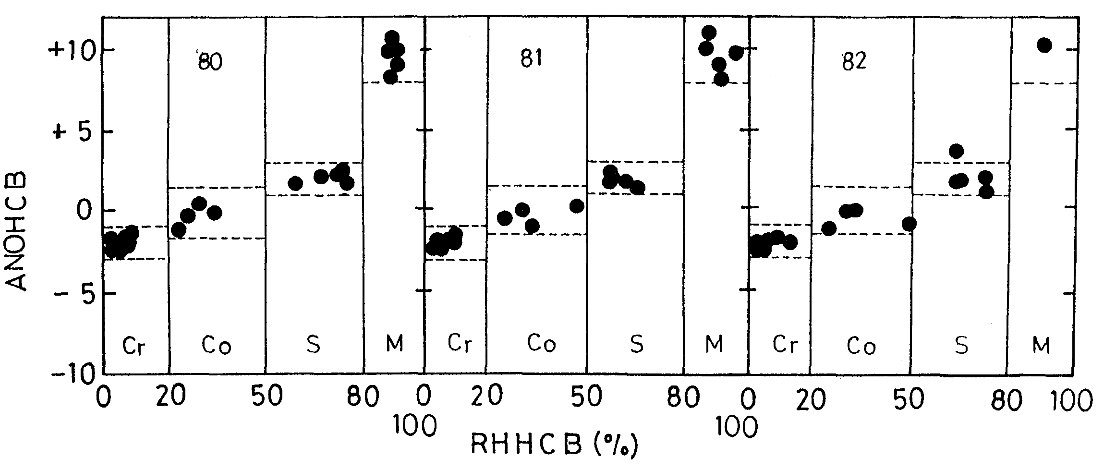

Fig. 6. Bud positions of *Sasa* are characteristic and constant in each types in the relation between RHHCB and ANOHCB. Cr, Co, S and M see Fig. 2. 80, 81 and 82 see Fig. 2.

and II) showed a similar tendency to the winter bud. In comparison to the winter bud, the spring bud was rather dominant from 0 to +5 in the second year. The spoiled bud was mostly observed in the first year and rather few in the second year. Eventually the 3-year-aged culms produced the winter bud only on the node order lower than –1, and some of branches in the upper parts begin to die off. Thus, from the bud emergent pattern the longevity of a culm in S type seemed to be four or five years (cf. Takakuwa and Ito 1986), and activation of the latent bud began with those of the central parts and spread to those on both sides (Fig. 8).

In Cr type the winter bud was formed from –3 to –1 in the first year. In the second and third year it enlarged below –2 near ground level (Fig. 7). All of the latent buds above the ground level changed to the winter bud in three years, and activation areas of the latent bud moved downward consecutively (Fig. 8). The range and number of the spring bud and the spoiled bud in Cr type was narrower and smaller than those in S type. The active bud (the winter bud + the spring bud) in S type was considerably more than that in Cr type as seen in Figure 7. In S type larger number of bud was dead. The rate of dead buds to the active bud was more than 60% in S type for at least 2 years; in Cr type it was less than 20%. Again, S type showed a larger rate of the spoiled bud than Cr type. These results indicated that in S type there were many active buds and then most of them were dead, and that in Cr type there are a few active buds and most of them survived to grow. The

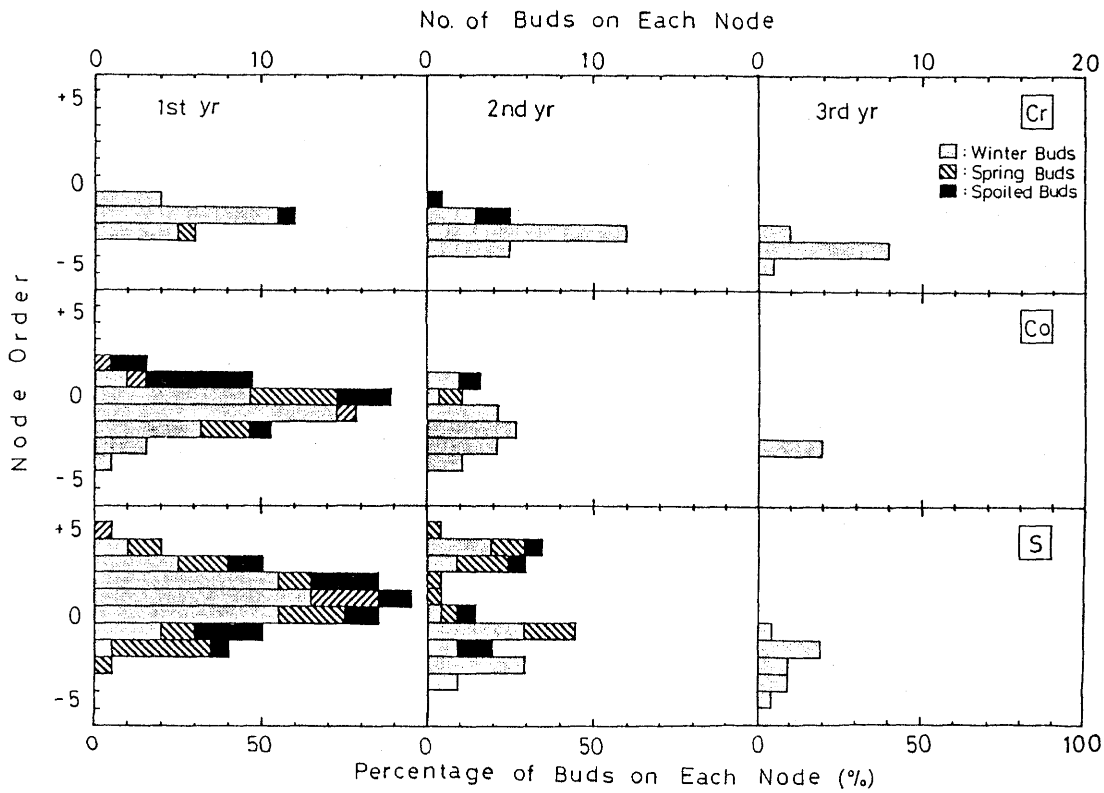

Fig. 7. Annual variation of node order of 3 kinds of buds, winter bud, spring bud and spoiled bud, from 1st year (1980) to 3rd year (1982). Cr, Co and S see Fig. 2.

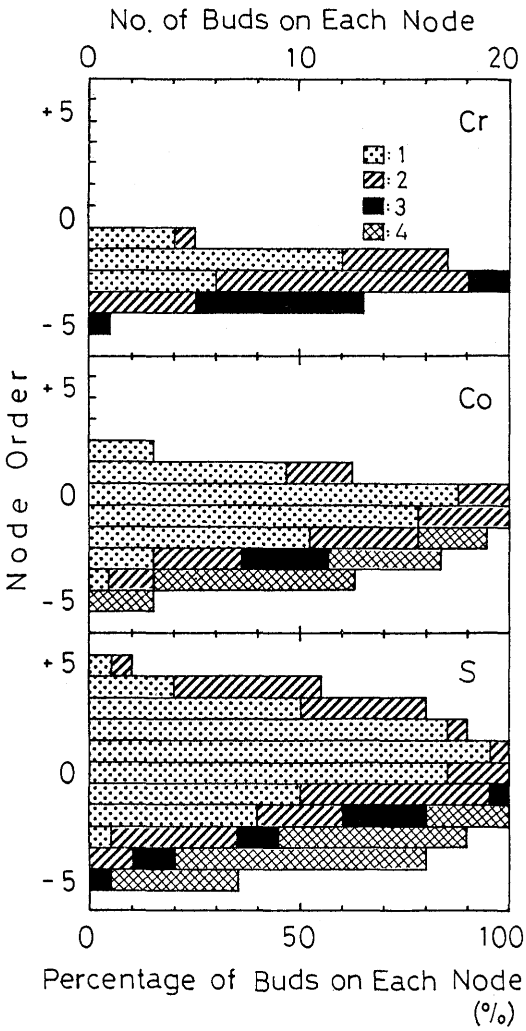

Fig. 8. Annual variation of node order of changed buds, which were active buds (winter buds + spring buds) from 1st year (1980) to 4th year (1983). 1: 1st year; 2: 2nd year; 3: 3rd year; 4: 4th year. Cr, Co and S see Fig. 2.

results were considered to be characteristic of branching of each types of *Sasa*. The typical form of S type is characterized by scattered branching due to the death of most of active buds, which issued branches throughout the culms; that of Cr type is characterized by a few, usually one or two, branches or shoots from the base.

In Co type, the winter bud emerged from –4 to +1 in the first year, and most of them appeared between –2 and 0 as seen in Figure 7. In the second year the bud reduced the number and appeared between –4 and +1 but mostly between –1 and –4. In the third year it appeared only at –3. The spring bud appeared from –2 to +2 in the first year and at 0 in the second year. In this type the rate of the spoiled bud to buds which changed to other types of bud was rather larger than the other 2 types in the first year. In addition, it was characteristic of this type in which buds in the third year was limited to one in number and at –3 in NDO. As activation areas of the latent bud moved gradually downward, this emergent pattern of buds was somewhat similar to Cr type (Fig. 8). On the other hand, the range and number of the spring bud and the spoiled bud was similar to that of S type. Consequently, this type was intermediate between S and Cr type in the emergent pattern.

Similar results have been obtained from *Sasa* plants in the following cases: (1) plants grown in different climatic conditions, (2) plants affected by human impacts such as cutting, spraying of herbicides, etc., and (3) plants in different microhabitual conditions such as sunshine duration, water content of soil, etc. From the results obtained, we can surmise that the emergent pattern of buds and relative number of them are fixed and controlled genetically.

Conclusional remarks

The elongation of internodes is principally intercalary in the Monocotyledons (Cutter 1971). It may be stimulated by some hormones and controlled genetically. There have been no data about the elongation of internodes of *Sasa* plants, but in the present work, a regularity of the elongation was observed by using the Node Order, although its physiological mechanism has not been clarified. From this, the Node Order is available to the comparison of bud position of different *Sasa* plants.

It is a well known fact that the branching type is characteristic of sections in the genus *Sasa*. The branching type results in the life form: sect. Crassinodi is the Hemicryptophyte, and sects. Sasa and Macrochlamys are the Nanophanerophyte. According to schematic figures of the branching types (Usui 1961, Suzuki S. 1961) buds on the culm concentrate on the base in section Crassinodi; they are distributed over the aerial culms and on underground in sections Sasa and Macrochlamys. However, when we use the Node order, the range of buds can be described clearly and quantitatively; −1 to −5 in Cr type, that is, descriptively near the base and underground; −5 to +5 in S type, that is, near underground to the top; and −9 to +14 in M type, that is, from underground to the top. The results are not contradictory to the traditional explanation of the branching type, and at least those 3 types are comparable to the 3 sections mentioned already; Cr type to section Crassinodi, S type to Sasa and M type to Macrochlamys. It is shown to be reasonable for the determination of the section to which a *Sasa* plant belongs by combining individual morphological characteristics with the Node Order (NDO).

This NDO is more effective in the distinction of each type in combination with the indexes RHHCB and ANOHCB, which are related to the highest bud position on the culms. In the actual formation of the branching type, however, the number of buds, the kind of buds and the longevity of shoots are related to each other as far as the present work is concerned. It is very curious that branches per culm (shoot) are fewer in S type than in Cr or Co type, but it is shown that the longevity of shoots is longer in the former than in the latter. The winter buds of S type, although most of them die, enlarge and add continuously new branches toward the upper parts during the following four or five years. Thus, we often experience to meet with a bush of single culms or very few branching culms or complicated branching culms of *S. senanensis* populations in the field.

Difficulty of *Sasa* classification is in uncertainty to recognize the individuality. In this meaning many species described, but not all the species, are rather a "museum species" (Kazaki and Okada 1958) but not a "biological species" (Solbrig 1970). Usui (1961) emphasized the practice of studies based on living populations. In fact, he recognized 3 taxa including 2 known taxa and one hypothetical taxon among 7 "species" distinguished by Nakai in Nikko. This working case is our case. Although we recorded characteristics or features of individual *Sasa* plants in the field, we neglected those species names in this work. This assemblages of *Sasa* investigated include several species described or listed in taxonomical or ecological references. Typical representative examples are: *Sasa amphitricha* Koidz., *S. apoiensis* Nakai, *S. arikai* Miyabe et Tatewaki, *S. cernua* Makino, *S. debilis* Nakai, *S. depauperata* Takeda, *S. kurilensis* Makino et Shibata, *S. kurilensis* var. *uchidai* Makino, *S. megalophylla* Makino et Uchida, *S. sylvatica* Tatewaki, *S. senanensis* Rheder, *S. yahikoensis* Makino, *S. yasokichii* Tatewaki et Tomooka, etc. Nevertheless, we can draw common features from the assemblages, and three types of *Sasa* surely correspond to the three known sections. It does not immediately prove that these types are identical to a specific status. However, the indexes designed are helpful to solve some problematic issues; according to the indexes, *S. depauperata,* which was published as a member of sect. Crassinodi, should belong to sect. Sasa; *S. cernua,* which is considered to be a hairy leaved species in sect. Macrochlamys is rather intermediate in the bud performance between Macrochlamys and Sasa.

There remain some issues of the bud performance. According to Hara (1981) there are two types of branching: one is sylleptic and the other is propolatic. Our observations show that most of *Sasa* are propolatic but in some cases they seem to be sylleptic. We have an expectation to clarify this difference by using and developing any quantitative treatments such as the NDO, the RHHCB, the ANOHCB, etc.

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要　旨

新指数節序とはササの稈上における節の番号順列である．ササ属の分類には稈の分枝様式が重視されるが，分枝は節に生ずる芽に由来する．このため分枝様式の比較には稈上の節の位置の確認と，異なる稈の間の節の位置の比較のために，一種の定量的基準が必要となる．筆者らはササの稈各節間の長さが全くでたらめに配列されていないことに着目し，通例唯1個認められる最長節間を節に番号づけをするための基準として選んだ．すなわち最長節間を構成する上下2個の節のうち，下方の節を0とし，それより上方の節に順次+1，+2，+3…，下方の節に−1，−2，−3…と番号づけし，これを節序と呼ぶこととした．この節序と1983年の筆者らの考案した相対最高着芽位置指数（稈上最高位につく芽の基部からの高さの全稈長に対する比）と併せ用いると，従来記述的に区分されていたササ属の3つのセクション，チシマザサ節，クマイザサ節，ミヤコザサ節の区分が一層客観的かつ定量的に示される．また芽について3つの種類，冬芽，春芽，放棄芽が認められるが，潜伏芽からこれらの芽に転じる部位を節序を用いて示すとやはりセクション間の特性を明確に示すことができる．このことから将来ササ属植物の研究に節序は有用性をもっていることが期待される．この研究を通じて，ミヤコザサ節とクマイザサ節との分布的な移行部には両者の中間的なタイプのササの存在が暗示され，これらのササに対してはcomposite typeと呼んで区別した．