Sexual and Asexual Reproduction of *Dicranum speirophyllum* (Dicranaceae, Bryophyta), Endemic to the Hawaiian Islands

Masanobu Higuchi

Department of Botany, National Museum of Nature and Science, Amakubo 4–1–1, Tsukuba, Ibaraki 305–0005, Japan E-mail: higuchi@kahaku.go.jp

(Received 5 December 2012; accepted 19 December 2012)

Abstract *Dicranum speirophyllum* Mont. is a dioicous moss endemic to the Hawaiian Islands. Sexual and asexual reproduction of *Dicranum speirophyllum* was studied at the field research of Hawaiian Islands in 1997, 1998 and 1999. Brood bodies are flagelliform branches which are only found in *D. speirophyllum* var. *breviflagellare* (Müll. Hal.) Bartr. The polysety of the species is firstly recorded and the frequency of polysety was investigated. Totally over 30% of the fertile shoots were polysetous in the material studied. The number of setae in a shoot varied from one to four, and one was the most common. The frequency of polysety was different among populations in a small area. The dwarf males were observed on the tomenta of the stems in the fertile population.

Key words: Bryophyta, *Dicranum speirophyllum*, dwarf male, Hawaiian Islands, polysety, reproduction.

Dicranum species are distributed mainly in temperate regions of the Northern Hemisphere. According to Bartram (1933) and Hoe (1974), there is recorded from the Hawaiian Islands one endemic species of *Dicranum*, *D. speirophyllum* Mont. This species has been known in Kauai, Oahu, Molokai, Maui and Hawaii Islands, and to be very variable in size and form; for example, four varieties are recognized (cf. Staples *et al.*, 2004).

This paper deals with the reproduction of *Dicranum speirophyllum* Mont. (Dicranaceae) (Fig. 1-1) based on the filed study and the specimens which were collected by the author and Dr. T. Arikawa during the expeditions to the Hawaiian Islands organized by the National Museum of Nature and Science, Tokyo in 1997, 1998 and 1999. Observations in the field and the laboratory based on the specimens of *Dicranum speirophyllum* were made to better understand its reproductive behavior.

The development of more than one sporophyte from a single gametoecium, each from separate archegonium, is known as polysety (cf. Magill, 1990). Most bryophytes typically show monosety, that is, a sporophyte develops in only one archegonium in each gametoecium. Thus polysety does not occur often or in every group of bryophytes. For example, Longton (1962) noted that polysety had been recorded in 66 British mosses (more than 10% of the British moss flora). Althought polysety in *Dicranum speirophyllum* has never been reported, it was found in *D. speirophyllum* var. *speirophyllum* from Hawaii Island for the first time (Fig. 1-2).

Materials and Methods

In Dicranum speirophyllum, four varieties are known, such as var. speirophyllum, var. breviflagellare (Müll. Hal.) Bartr., var. condensatum (Sull.) Wijk & Marg. and var. elongatum (Sull.)



Fig. 1. *Dicranum speirophyllum* Mont. var. *speirophyllum*. 1. Plants with sporophytes showing the LCI stage.
2. Shoots with 1–3 mature sporophytes showing the LCI stage. Leaves removed to show the gametoecia. Scales in 1 mm. 3. Dwarf males growing on the tomenta of stem. 4. Male bracts, mature antheridium and paraphyses.

Wijk & Marg. Hoe (1974) pointed out, "Both the var. *condensatum* and var. *elongatum* of Sullivant have been accepted by the *Index Muscorum* but do not appear anywhere in the recent Hawaiian bryological literature. Judging from their original descriptions, these two varieties are apparently little more than ecomorphs of this very variable species and probably will be shown to be synonyms when further investigated." The author agrees the comment by Hoe (1974), that is, var. *condensatum* and var. *elongatum* are not recognized here. Only small plants with brood body are distinguished from var. *speirophyllum* as var. *breviflagellare*. The habitats and substrates were recorded in each cite.

In Hawaii Island, all fertile shoots of D. speirophyllum var. speirophyllum were examined for investigating the habit of polysety from six populations in the field (P1-P6) which were different in size and discontinuously dispersed over a small area (ca. 20×20 m) in South Hilo District, Hilo Forest Reserve, 16 miles west of Hilo, 1200 m alt. (19°42'N, 155°17'E), 18 June 1999. The methods used for this study follow those of Higuchi (1997), but some different points are annotated. In Dicranum speirophyllum var. speirophyllum showing successive growth, the parts of plant formed year by year can be recognized. The old setae of the previous year were ignored. When a shoot is branched (cf. Fig. 1-2), they were counted individually.

Twenty six specimens examined in this study are deposited in the herbaria of the National Museum of Nature and Science, Tokyo (TNS) and the Bernice P. Bishop Museum (BISH).

Dicranum speirophyllum Mont. var. speirophyllum

Specimens examined. Hawaii Islands. **Kauai Isl.**, Waimea Dist., Alakai Swamp, along Mohihi Taril, 1000–1200 m alt. (22°07'N, 159°35'E), on rotten stump, 20 October 1997, Higuchi 32659; Kokee State Park, along Awaawapuhi Taril, 1180 m alt. (22°09'N, 159°39'E), on root, 23 October 1997, Higuchi 32773.

Molokai Isl., Molokai Dist., Pepeopae,

1200 m alt. (21°07'N, 156°54'E), on humus, 3 November 1997, Higuchi 33037; 1170 m alt., on humus, 12 November 1997, Higuchi 33259.

Maui Isl., Makawao Dist., ca. 3 km ENE of Olinda, Olinda Flume, 1280 m alt. (20°48'N, 156°14'E), on humus, 18 June 1998, Arikawa 943.

Hawaii Isl., South Hilo Dist., Hilo Forest Reserve, 16 miles west of Hilo, 1200 m alt. (19°42'N, 155°17'E), on humus, 30 May 1999, Higuchi 33482, 33517; Hilo Forest Reserve, 16 miles west of Hilo, 1200 m alt. (19°41'N, 155°18'E), on humus, Higuchi 34248; North Kona Dist., Makaula-Ooma Mauka Tract Forest Reserve, 1000 m alt. (19°43'N, 155°57'E), on decayed log, 16 June 1999, Higuchi 34149; South Kohara Dist., Upper Hamakua Ditch Trail, 1150m alt. (20°04'N, 155°40'E), on humus, 11 June 1999, Higuchi 33986; Kau Dist., Kapapala Forest Reserve, along Ainapo Trail, 1100m alt. (19°22'N, 155°28'E), on humus, 1 June 1999, Higuchi 33589, 33590; 1580m alt., on treetrunk, Higuchi 33593; on root, Higuchi 33594; 1670 m alt., on tree-trunk, Higuchi 33602.

Dicranum speirophyllum Mont. var. *breviflagellare* (Müll. Hal.) Bartr.

Specimens examined. Hawaii Islands. **Kauai Isl.**, Waimea Dist., Alakai Swamp, along Mohihi Taril, 1000–1200 m alt. (22°07′N, 159°35′E), on humus, October 1997, Higuchi 32678; on treetrunk, Higuchi 32729.

Molokai Isl., Molokai Dist., Puu Kolekole, 1100 m alt. (21°06'N, 156°55'E), on humus, 4 November 1997, Higuchi 33063; on fallen log, Higuchi 33128; Pepeopae, 1200 m alt. (21°07'N, 156°54'E), on tree-trunk, 5 November 1997, Higuchi 33132.

Maui Isl., Makawao Dist., ca. 3 km ENE of Olinda, Olinda Flume, 1280 m alt. (20°48'N, 156°14'E), on tree-trunk, 18 June 1998, Arikawa 941.

Hawaii Isl., South Hilo Dist., Hilo Forest Reserve, 16 miles west of Hilo, 1200 m alt. (19°42'N, 155°17'E), on humus, 30 May 1999, Higuchi 33485; on tree-trunk, 18 June 1999, Higuchi 34239; Upper Waiakea Forest Reserve, along Stainback HWY, 1360 m alt. (19°33'N, 155°16'E), on base of tree, 3 June 1999, Higuchi 33693; South Kohara Dist., Kohara Mts., Puu O Umi Natural Area Reserve, 1570 m alt. (20°04'N, 155°43'E), on rotten log, 13 June 1999, Higuchi 34013; 1515 m alt., 155°43'E), on tree-trunk, Higuchi 34002.

Results and Discussion

According to Staples *et al.* (2004), *Dicranum speirophyllum* var. *speirophyllum* is known from Kauai, Oafu, Molokai, Maui and Hawaii Islands and var. *breviflagellare* from Oafu, Maui and Hawaii Islands. The latter, var. *breviflagellare*, is newly recorded from Kauai and Molokai Islands.

Asexual reproduction

Dicranum speirophyllum grows on higher than 1,000 m alt. in wet forest in the Hawaiian Islands. The plant size is may be related to their habitat,

that is, the plant growing on humus is usually larger than the plant growing on tree-trunk which is usually affected by drought. Bartram (1933) considered that this small plants with brood body as variety of the species, *D. speirophyllum* var. *breviflagellare*. The brood body is flagelliform branches with distant, scale-like, small, ecostate leaves in the axils of the upper leaves, and it is easy to fall down.

Sexual reproduction

Sporophytes were found in the specimens of *D. speirophyllum* var. *speirophyllum* and var. *breviflagellare* from Hawaii Islands except one of var. *speirophyllum* from Kauai Island (Table 1). Most sporophytes were in the Early Calyptra Intact (ECI) stage and the Late Calyptra Intact (LCI) stage as defined by Greene (1960). In the ECI stage the capsule is not expanding and has the same diameter as the seta. In the LCI stage the capsule is expanding or has attained full size.

Table 1. Reproductive condition of each specimens of *Dicranum speirophyllum* var. *speirophyllum* and var. *breviflagellare*

| | Island | Flagelliform branches | Sporophytes | Dwarf male | Substrate | Specimen number |
|----------------------------|---------|--------------------------|-------------|---------------|--------------|-----------------|
| Dicranum speirophyllum van | Kauai | | | | rotten stump | Higuchi 32659 |
| speirophyllum | Kauai | _ | monosety | — | root | Higuchi 32773 |
| | Molokai | _ | | — | humus | Higuchi 33037 |
| | Molokai | _ | — | — | humus | Higuchi 33259 |
| | Maui | | — | _ | humus | Arikawa 943 |
| | Hawaii | _ | polysety | + | humus | Higuchi 33482 |
| | Hawaii | — | polysety | + | humus | Higuchi 33517 |
| | Hawaii | — | polysety | + | humus | Higuchi 34248 |
| | Hawaii | | _ | _ | decayed log | Higuchi 34149 |
| | Hawaii | — | | | humus | Higuchi 33986 |
| | Hawaii | — | | | humus | Higuchi 33589 |
| | Hawaii | — | — | _ | humus | Higuchi 33590 |
| | Hawaii | — | | _ | tree-trunk | Higuchi 33593 |
| | Hawaii | — | | _ | root | Higuchi 33594 |
| | Hawaii | — | — | _ | tree-trunk | Higuchi 33602 |
| Dicranum speirophyllum van | . Kauai | + | | | humus | Higuchi 32678 |
| breviflagellare | Kauai | + | | _ | tree-trunk | Higuchi 32729 |
| | Molokai | + | | _ | humus | Higuchi 33063 |
| | Molokai | + | — | _ | fallen log | Higuchi 33128 |
| | Molokai | + | | _ | tree-trunk | Higuchi 33132 |
| | Maui | + | — | _ | tree-trunk | Arikawa 941 |
| | Hawaii | + | monosety | + | humus | Higuchi 33485 |
| | Hawaii | + | monosety | + | tree-trunk | Higuchi 33239 |
| | Hawaii | + | | — | base of tree | Higuchi 33693 |
| | Hawaii | + | monosety | + | rotten log | Higuchi 34013 |
| | Hawaii | + | | _ | tree-trunk | Higuchi 34002 |

| Population | | T-4-1 | | | |
|------------|------|-------|-----|-----|---------|
| | 1 | 2 | 3 | 4 | - Total |
| P1 | 204 | 48 | 1 | 0 | 253 |
| % | 80.6 | 19 | 0.4 | | |
| P2 | 279 | 56 | 0 | 0 | 335 |
| % | 83.3 | 16.7 | | | |
| P3 | 331 | 65 | 0 | 0 | 396 |
| % | 83.6 | 16.4 | | | |
| P4 | 413 | 40 | 0 | 0 | 453 |
| % | 91.2 | 8.8 | | | |
| P5 | 491 | 345 | 10 | 0 | 846 |
| % | 58 | 40.8 | 1.2 | | |
| P6 | 612 | 580 | 65 | 1 | 1258 |
| % | 48.6 | 46.1 | 5.2 | 0.1 | |
| Total | 2330 | 1134 | 76 | 1 | 3541 |
| % | 65.8 | 32 | 2.2 | | |

Table 2. Number of shoots with 1–4 setae in Dicranum speirophyllum

The development of sporophytes in a gametoecium was almost synchronous (Fig. 1-2).

Polysety was found in D. speirophyllum var. speirophyllum from Hawaii Island. Table 2 shows the frequency of polysety in Dicranum speirophyllum. The frequency of polysety was rather different among six populations. In each population 8.8% to 51.4% of the fertile shoots were polysetous, and totally over 34.2% of the fertile shoots were polysetous. The number of setae in a gametoecium varied from one to four, which is almost not in accord with the description, "seta solitary," by Bartram (1933). The most frequent number of setae per gametoecium was one in all population. Totally one seta per gametoecium was the most common. The number of setae per shoot seemed to rise proportionately with increase in the number of fertile shoots examined.

Polysety in *Dicranum majus* was studied by Sowter (1951) and Hughes (1980). Sowter (1951) reported by examining 297 shoots that (1) about 67% of the fertile shoots were polysetous, (2) the number of setae in a gametoecium varied from one to six and (3) two is the most common. While Hughes (1980) recorded by examining 287 shoots that (1) about 55% of the fertile shoots were polysetous, (2) the number of setae in a gametoecium varied from one to five and (3) one is the most common. On the other hand, Higuchi (1997) studies polysety in Dicranum polysetum Sw. and reported by examining 848 shoots that (1) about 80% of the fertile shoots were polysetous, (2) the number of setae in a gametoecium varied from one to six and (3) three is the most common. As compared with Dicranum majus and D. polysetum, D. speirophyllum var. speirophyllum shows lower degree of polysety. The frequency of polysety in Dicranum polysetum (Higuchi, 1997) was different among seven populations in a small area. The result gained in this study of Dicranum speirophyllum var. speirophyllum supports an idea that the frequency of polysey is more or less unstable in a small area.

In some dioicous mosses, the tiny male gametophyte usually borne on the female plant is called as dwarf male (cf. Magill, 1990). The dwarf male is found in species of some moss genera, e.g., Dicranum, Hypnum, Macromitrium, etc. Recently Pichonet and Gradstein (2012) reviewed the male dwarfism in Dicranum. They noted that male plant status of D. speirophyllum is unknown. Bartram (1933), however, reported the dwarf male in Dicranum speirophyllum. Because Bartram (1933) described it as "Male plants minute, 1 mm, or less, high, attached to the tomentum of the stems of the fertile plants." The dwarf male is not so commonly observed in the species. The dwarf males were observed on the tomenta of the stem in the population with sporophytes (Figs. 1-3, 4), while they were not found in the sterile population. Although the data are a few, the dwarf male possibly leads to frequent sexual reproduction.

Acknowledgments

I wish to express my sincere thank to Dr. H. Kashiwadani of the National Museum of Nature and Science for giving the opportunity to join the field research and Prof. C. W. Smith of University of Hawaii and Dr. T. Arikawa for their kind help in the field research. This study was supported by a Grant-in-Aid (No. 09041169 to Kashiwadani) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

References

- Bartram, E. B. 1933. Manual of Hawaiian Mosses. Bishop Museum Bulletin 101. 275 pp.
- Greene, S. W. 1960. The maturation cycle, or the stages of development of gametangia and capsules in mosses. Transactions of the British Bryological Society 3: 736– 745.
- Higuchi, M. 1997. Studies of polysety in *Dicranum polysetum* (Dicranaceae, Musci). Annals of the Tsukuba Botanical Garden 16: 129–133.
- Hoe, W. J. 1974. Annotated checklist of Hawaiian mosses. Lyonia 1: 1–45.
- Hughes, J. H. 1980. The relation between the occurrence

of polysety and the number of archegonia in the female inflorescences of *Dicranum majus* and *D. scoprium*. Journal of Bryology 11: 337–342.

- Longton, R. E. 1962. Polysety in the British Bryophyta. Transactions of the British Bryological Society 4: 326– 333.
- Magill, R. E. (ed.) 1990. Glossarium Polyglottum Bryologiae. 297 pp. Missouri Botanical Garden, St. Louis.
- Pichonet, A. and Gradstein, S. R. 2012. Male dwarfism in the genus *Dicranum* (Dicranaceae) — a review. Cryptogamie, Brologie 33(3): 29–311.
- Sowter, F. A. 1951. The polysetous inflorescence of *Dicranum majus* L. Transactions of the British Bryological Society 1: 73–74.
- Staples, G. W., Imada, C. T., Hoe, W. J. and Smith, C. W. 2004. A revised checklist of Hawaiian mosses. Tropical Bryology 25: 35–69.