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Phyllotaxis on the Main Shoot of Wild Tomato Plants Calculated by the Parastichy System

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Summary

Phyllotaxis on the main shoot of tomato plants, *Lycopersicon pimpinellifolium* (Jusl.) Mill., was studied by the parastichy system. Three, five, or eight contact parastichies were identified. The direction of winding of the spirals when there were three parastichies was the same as that of the genetic spiral, but opposite when there were five parastichies. Both patterns were found when there were eight parastichies. The angle of divergence between each pair of leaves in contact parastichies was less with eight parastichies than with three or five parastichies. Eight parastichies were not easy to see in the tomato plants, because these plants developed only 10 to 13 leaves on their main shoot. Three and five parastichies were easier to identify than eight parastichies. Phyllotaxis by the parastichy system could be identified in all the tomato plants observed. We concluded that the parastichy system was more suitable than the orthostichy system to represent the phyllotaxis of tomato plants, because the tomato plants had a wide range of leaf arrangements in individuals and in different plants.

From these reasons, phyllotaxis on the main shoot was found to be 3 and 5, 3 : 5, or 3+5. When we need to show by the orthostichy system, phyllotaxis of 3/8 with 135 degrees could be used as a typical arrangement of leaves.

The phyllotaxis of tomato plants has been calculated to be 3/8 by the orthostichy system, because the angle of divergence between each pair of leaves on the main shoot of the plants is about 135 degrees (2). This means that the leaves on the main shoot of tomato plants arrange in a mean of eight orthostichies. In general, most leaves do not arrange exactly on these eight lines, and the tomato plants studied developed only 9-12 leaves on the main shoot. It is necessary to study the phyllotaxis of tomato plants when there are more leaves on the main shoot, or by another method, such as the parastichy system. Phyllotaxis evaluated by the parastichy system is a "convenient method to explain the phyllotaxis on a dwarf stem" (12). Even when divergence angle changed a little between each pair of leaves or each plant, phyllotaxis is represented as same value by parastichy system. On the other hand, even when the divergence angle remains constant, phyllotaxis by parastichy system changes with the number of leaves on a shoot (8).

In this experiment, parastichy system was employed to calculate the phyllotaxis on the main shoot of tomato plants that had elongated stems. As in previous paper (2), a related wild species *L. pimpinellifolium* was used for the observations.

Materials and Methods

Seeds of a wild variety of tomato, *Lycopersicon pimpinellifolium* (Jusl.) Mill. PI 133542, were germinated in August 1991. Plants were grown in clay pots 12 cm in diameter. The plants that developed flowers on the apex of a main shoot with 10 to 13 leaves were studied. All of the primary lateral shoots on the main shoot were removed before the first flower on the first inflorescence opened. When the first flower opened, all leaflets in each compound leaf were removed so that the number and the direction of winding of the spirals (parastichies) could be identified by the parastichy system. The number of parastichies in each plant was calculated as the number of contact parastichies. Spirals with the same (opposite) direction of winding as that of the genetic spiral in the same plant were called plus (minus), and recorded by the symbol $+(-)$. Five, 37, 52, and six plants with 10, 11, 12, and 13 leaves, respectively, on the main shoot were studied. The arrangement of leaves on the genetic spiral was programmed on a micro-computer to represent the contact parastichies.

Results and Discussion

When we represented the phyllotaxis of tomato plants by the parastichy system, contact parastichies with three, five, or eight spirals were identified on the main shoot of plants with 11 leaves (Table 1). Regardless of the direction of winding of the genetic spiral, the direction of winding of three parastichies was the same as that of a genetic spiral, so that the type of winding of parastichies with three spirals was represented as $3+$. The direction of winding of five parastichies was opposite, and was represented as $5-$. With eight spirals, some were $8-$ and some were $8+$. Plants with three spirals with winding opposite to that of the genetic spiral $(3-)$ and plants with five spirals with winding of the same direction as that of the genetic spiral $(5+)$ were not found. The same patterns were found in plants with 12 (Table 2), 10 and 13 leaves (data not shown).

TABLE 1. *Angle of Divergence*[b] *between Adjoining Pairs of Leaves in Parastichies on the Main Shoot of Tomato Plants with 11 Leaves*

Type of parastichy[a]	Number of parastichies			Number of plants
	3	8	5	
3−	—	—	—	
3+	31.3±2.3[b]	−38.3±6.7	−69.7±4.8	3
8−	39.8±1.2	−14.6±3.5	−55.1±2.0	12
8+	49.7±0.8	14.7±2.7	−37.6±1.6	18
5−	58.8±1.3	36.3±5.1	−24.4±3.1	4
5+	—	—	—	

[a] The kind of parastichy was decided from the smallest value of the angle of divergence in each parastichy.
+ and − : Direction of winding of parastichies. +, Same direction as that of the genetic spiral; −, opposite direction to that of the genetic spiral.

[b] Mean±SE.

TABLE 2. *Angle of Divergence*[b] *between Adjoining Pairs of Leaves in Parastichies on the Main Shoot of Tomato Plants with 12 Leaves*

Type of parastichy[a]	Number of parastichies			Number of plants
	3	8	5	
3−	—	—	—	
3+	—	—	—	
3+ or 8−	33.8±2.0[b]	−36.0±5.5	−65.7±3.7	6
8−	39.2±0.9	−15.7±2.5	−54.5±1.6	23
8+	50.4±1.0	12.8±2.3	−38.2±1.4	17
8+ or 5−	54.8±1.9	28.1±5.9	−29.3±3.9	2
5−	56.6±2.0	36.3±4.8	−22.9±2.5	4
5+	—	—	—	

[a),b)] See Table 1.

The relationship between the number and direction of winding of contact parastichies was as follows. When leaves were arranged at angles of divergence of 120, 135, or 144 degrees, the phyllotaxis is identified as being 1/3, 3/8, or 2/5 with three (Fig. 1B), eight (Fig. 1E), or five (Fig. 1H) orthostichies, and the type of parastichy is represented as 3±, 8±, or 5±, respectively. When the leaves arranged at angles less than 120, 135, or 144 degrees, the phyllotaxis is identified as being of contact parastichies of three, eight, or five spirals with an opposite direction of winding to that of the genetic spiral, and the type of parastichy is represented as 3− (Fig. 1A), 8− (Fig. 1D), or 5− (Fig. 1G), respectively. When the leaves arranged at angles greater than 120, 135, or 144 degrees, the phyllotaxis

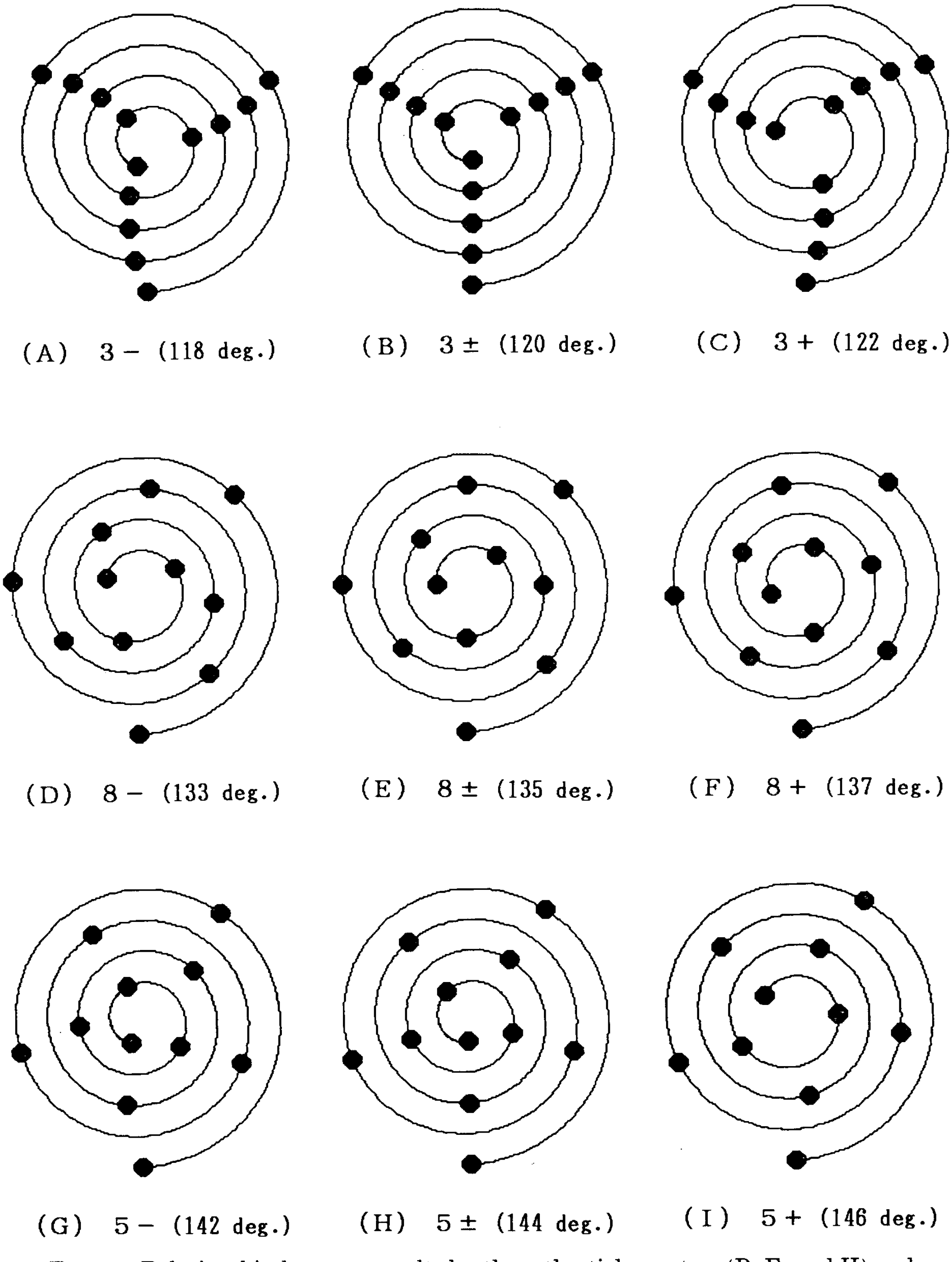

FIG. 1. Relationship between results by the orthostichy system (B, E, and H) and the parastichy system (A, C, D, F, G, and I). B, E, and H: Arrangement of leaves with angles of divergence of 120, 135, and 144 degrees, respectively. A (and C), D (and E), and G (and I): Examples of three, eight, and five parastiches with angle of divergence greater than (less than) 120, 135, and 144 degrees, respectively. Direction of winding of the genetic spiral is shown as left-handed phyllotaxis (counterclockwise).

is identified as being of contact parastichies of three, eight, or five spirals with the same direction of winding as that of the genetic spiral, and the type of parastichy is represented as 3+ (Fig. 1C), 8+ (Fig. 1F), or 5+ (Fig. 1I), respectively. In our experiment, four kinds of contact parastichies were found: 3+, 8−, 8+, and 5− (Table 1 and Table 2). This showed that leaves of tomato plants arranged on the main shoot at angles of from 120 to 144 degrees. The angle of divergence between pairs of leaves in each type of parastichy of 8− and 8+ was less than that of 3+ or 5−, and the number of plants of these kinds was greater than that of plants with 3+ or 5−. But the eight spirals could not be identified clearly, because the number of leaves on the main shoot was too few for identification of contact parastichies as eight spirals. On the other hand, the angle of divergence between pairs of leaves in each parastichy of 3+ and 5− was greater than that of 8− and 8+, but parastichy of 3+ and 5− was identified clearly. From these results, the phyllotaxis of tomato plants with 10 to 13 leaves on the main shoot seemed to be 3 and 5, 3 : 5, or 3+5 by the parastichy system.

The phyllotaxis of tomato plants was calculated to be 3/8 by the orthostichy system in our previous paper (2). The mean angle of divergence of tomato plants, 135.3 degrees (shown from that paper in Fig. 2A here) was similar to the mean angle of divergence of the phyllotaxis of 3/8 (Fig. 2B) and to the phyllotaxis with the limiting value of the main series in Schimper-Braun's law (about 137.5 degrees; Fig. 2C). We can see not only eight orthostichies but also three and five contact parastichies in a plant with phyllotaxis of 3/8 with 11 leaves (Fig. 2B), and only eight orthostichies in a plant with 41 leaves (Fig. 2D). On the other hand, the arrangement of leaves with phyllotaxis of the limiting value of the main series in Schimper-Braun's law with 11 leaves had three and five contact parastichies (Fig. 2C), and that with 40 leaves had eight and 13 contact parastichies (Fig. 2E). When plants had 10 or 11 leaves, our results (Fig. 2A) were similar not only to a phyllotaxis of 3/8 (Fig. 2B) but also to a phyllotaxis of the limiting value of the main series in Schimper-Braun's law (Fig. 2C). In our experiment, about equal numbers of plants with 8− and 8+ were found (Table 1 and Table 2). That is, the numbers of plants with an angle of divergence more than 135 degrees and less than 135 degrees were observed as the same frequency. If the typical phyllotaxis has the limiting value of the main series in Schimper-Braun's law, the number of tomato plants with phyllotaxis of 8+ by the parastichy system would be more than the number of plants with phyllotaxis of 8−. Our results did not suggest this tendency, although they did not exclude its possibility.

In rare cases, leaves arranged in three, four, or five orthostichies. If these plants were the only specimens, the phyllotaxis of tomato plants would be taken to be 1/3 by the method of Ohkouchi (5), the orixate type by the method of Shishido and Hori (9) and by Usugami (10), or 2/5 by the method of Hayward (1), Lehman (3), McCollum and Skok (4), Picken *et al.* (6), Russell and Morris (7), and

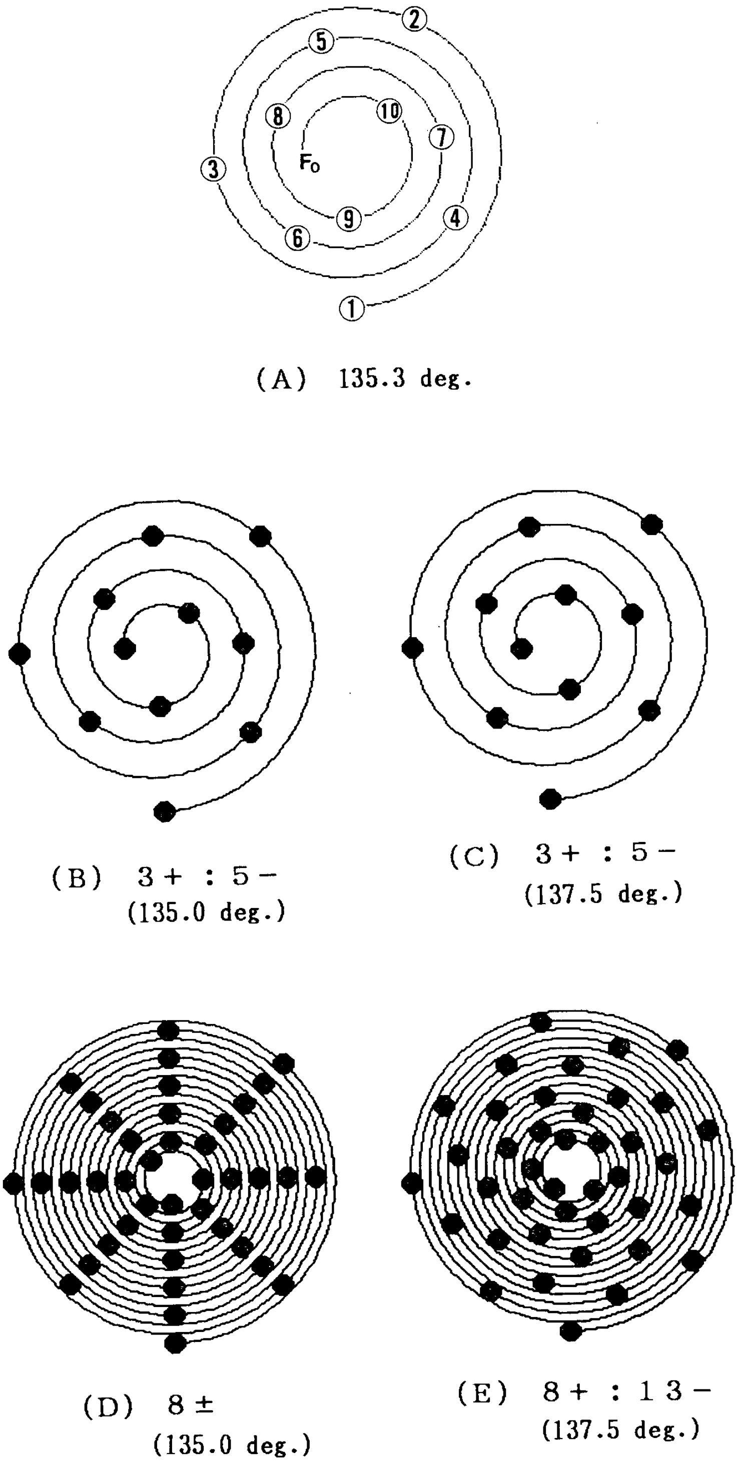

FIG. 2 Arrangement of leaves on the main shoot of tomato plants with left-handed phyllotaxis. A: Mean of 15 plants with 10 leaves cited from Kanahama *et al.* (2). B and D: Phyllotaxis of 3/8 with 11 and 41 leaves, respectively. C and E: Phyllotaxis of the limiting values on the main series of Schimper-Braun's law (about 137.5 degrees) with 11 and 40 leaves, respectively.

Yakuwa and Shiraki (11). Even when the leaves were arranged on eight orthostichies with a few leaves (10 to 13 leaves) on the main shoot, we could identify three and five parastichies clearly. When the angle of divergence of three spirals approached 120 degrees, the arrangement of leaves would be identified as being of a phyllotaxis of 1/3. And when the angle approached 144 degrees, the arrangement would be identified as being of a phyllotaxis of 2/5 (Fig. 1). If the typical phyllotaxis of tomatoes was 1/3, plants with parastichies of three spirals of both types, 3− and 3+, would occur in the same proportion. In the same way, if the typical phyllotaxis was 2/5, plants with five spirals of both types, 5− and 5+, would occur in the same proportion. Because plants with 3− or 5+ were not found in our observations, the possibility of phyllotaxis of 1/3 or 2/5 was ruled out. As mentioned above, tomato plants had a wide range of leaf arrangements in individuals and in different plants. Few leaves were exactly on the orthostichies. Thus, the parastichy system was more suitable than the orthostichy system to represent the phyllotaxis of tomato plants. By the parastichy system, the phyllotaxis on the main shoot of tomato plants was found to be 3 and 5, 3 : 5, or 3+5. When we need to calculate the angle of divergence between pairs of leaves in the genetic spiral by the orthostichy system, 135 degrees could be used as a typical angle of divergence. This value was the same as the angle of a phyllotaxis of 3/8.

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