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Reproductive strategy and morphological variation in *Trientalis europaea*

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Vegetative apomixis by rhizomes is shown to be the effective mode of reproduction in *Trientalis europaea* L. Rhizome development, morphology and biology are described in detail. Seed reproduction is only of minor, if any, importance in terms of survival of populations, but can bring a modicum of change to the genetically static clones. A limited amount of autogamy was experimentally proven. Variation in five morphological characters was assessed. Taxonomic, karyological and microevolutionary implications are briefly discussed.

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Die vegetative Apomixis mittels des Rhizoms wird als erfolgreiche Fortpflanzungsmethode bei *Trientalis europaea* L. nachgewiesen. Die Rhizomentwicklung, -morphologie und -biologie werden im Detail beschrieben. Die Vermehrung durch Samen ist von untergeordneter bzw. von keiner Bedeutung für das Überleben der Populationen, obwohl sie geringfügig zur Änderung der genetisch statischen Klone beitragen kann. Autogamie konnte in beschränktem Maße experimentell nachgewiesen werden. Ferner wurde die Variation von fünf morphologischen Merkmalen untersucht. Taxonomische, karyologische und mikroevolutionäre Schlußfolgerungen werden kurz diskutiert.

Keywords: *Trientalis europaea*, vegetative apomixis, seed reproduction, biology, morphological variation.

Introduction

Trientalis L. is a small primulaceous genus of which only four closely related species are on record: *T. europaea* L. (boreal and temperate Europe, from Iceland and Scotland through Central Europe and Siberia to Japan and northwestern North America), *T. borealis* RAFIN. (eastern North America), *T. arctica* FISCH. (eastern Siberia, Russian Far East, Japan, North America) and *T. latifolia* HOOK. (Pacific North America). A fifth species, *T. americana* PURSH, is considered to be synonymous with *T. borealis* RAFIN. (ANDERSON & LOUCKS 1973). All are low and glabrous perennials having slender rhizomes and simple erect stems bearing 0-5 small alternate leaves below and a whorl of larger leaves at the summit. The corolla is spreading and flat, without a distinct tube, divided deeply almost to the base, 6-9-merous.

Since PAX & KNUTH (1905), no attempt at a modern monograph or a revision has been made, and in Europe, *T. europaea* L. can hardly be a source of confusion to botanists.

However small and inconspicuous, though, the genus raises many interesting questions. One has to wonder, for instance, why its flowers are (predominantly) heptamerous, a number so rare in the plant kingdom, and why there is such an amazing degree of polyploidy. And why, in view of this condition, is there no evidence of gametophytic apomixis? The present paper seeks to answer at least some of these queries.

Material and methods

Field observations were carried out at nine sites (Tab. 1) located in seven mountain systems of the Bohemian Massif (nos. 2-3 and 5-9 belonging to the Sudeten Mts.). Fifty individuals per site were examined. Considering the peculiar mode of reproduction, care was taken to ensure that the aerial parts sampled were at least 1 m apart from each other. Of the morphological characters, the following were recorded: number of cauline leaves, number of leaves in the terminal whorl, length of the longest leaf, number of flowers, and number of corolla segments. For convenience, the material was referred to the three forms delimited ad hoc by MEDWECKA-KORNAŚ (1963): normal (N), diminutive (D) and ramose (R). Plants intermediate between N and D or N and R were classed as transitional (T). Rare cases (only two in the entire set of 450) in which one flower of a plant produced seed whereas the other did not, were disregarded. For practical reasons, the areas sampled had to be chosen in sites with sparse or no cover of other herbs (i.e. to enable the study of the tender rhizomes). Thus, the sets of plants for which the ratio sterile/fertile was determined were of necessity different from those in which morphological variation was studied several weeks earlier. To study the breeding behaviour, whole patches of plants were covered by fine muslin and left undisturbed for four weeks. Wherever possible, the term "plant" is avoided throughout this paper; if used, it denotes the aerial shoot. In this article "sterile" means flowering but not yielding any seed.

Tab. 1: List of topodemes sampled. — Liste der untersuchten Topodeme.

no.	Locality	2n
1	Bohemia: Krušné hory Mts., spruce forest on the southern hill-side of Mt. Klínovec, above Suchá, 960 m	

2	Bohemia: Krkonoše Mts., Velká Kotelná jáma glacial cirque, in *Pinus mugo* scrub, 1050 m	
3	Bohemia: Krkonoše Mts., in spruce forest just east of Velká Kotelná jáma glacial cirque, 950 m	
4	Bohemia: Žd'árské vrchy Mts., spruce forest between the village of Račín and Velké Dářko pond, 650 m	
5	Bohemia: Orlické hory Mts., spruce forest in the summit area of Mt. Malá Deštná, 1090 m	160[1]
6	Moravia: Kladský Sněžník Mts., spruce forest on the SE slope of Mt. Kladský Sněžník, 1350 m	
7	Moravia: Rychlebské hory Mts., spruce forest in the summit area of Mt. Smrk, 1125 m	
8	Moravia: Hrubý Jeseník Mts., dwarfed spruce forest on the northeast slope of Mt. Petrovy kameny, 1380 m	
9	Moravia: Hrubý Jeseník Mts., Na skřítku peat bogs, 920 m	

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[1] Counted by Dr. Andrzej JANKUN, Institute of Botany, Jagiellonian University, Kraków

Note: Register of German topographical names (in current use before 1945):

Hrubý Jeseník = Hochgesenke
Kladský Sněžník = Glatzer Schneeberg
Klínovec = Keilberg
Krkonoše = Riesengebirge
Krušné hory = Erzgebirge
Malá Deštná = Deschneier Kleinkoppe
Na skřítku = Berggeist
Petrovy kameny = Peterssteine
Rychlebské hory = Reichensteiner Gebirge
Smrk = Fichtlich
Suchá = Dürnberg
Orlické hory = Adlergebirge
Velká Kotelná jáma = Grosse Kesselgrube

Breeding behaviour

The examination of sexual reproduction yielded a confusing result. Table 2 shows that *Trientalis* plants remain largely sterile, but not to the degree indicated in the available literature. In the material studied, the proportion of sterile individuals ranged from 24 % to 84 %. There are only a few seeds per capsule and their viability proved to be poor under laboratory conditions, thus confirming results obtained by MATTHEWS (1941). It remains unclear whether the sterility is due to scarce visits by pollen vectors or to some intrinsic factors, such as poor viability of the pollen.

Autogamy has long been suspected (e.g. LÜDI 1926) and is technically feasible (the proterogynous flowers close towards the end of the flowering so that the introrse anthers are pressed to the still receptive stigma), but so far no attempt seems to have been made to prove it experimentally. The present author therefore undertook a pilot study of autogamous behaviour in topodeme no. 3 (chosen at random). The result was quite surprising: of 50 flowers isolated (for convenience, the number of plants was disregarded in this case), three (belonging to three different aerial stems) produced morphologically good seed.

It can be inferred, therefore, that seed production is considerably hampered in the topodemes studied. Of the investigated plants (total: 450), all bore remnants of last year's rhizomes, thus revealing their mode of origin. Not a single plant arisen from seed was recorded. Sexual reproduction is obviously of little importance in terms of survival of the populations, but could bring at least a modicum of change to the genetically static clones.

Vegetative reproduction

Effective reproduction is by vegetative spread: thin rhizomes with a tuber-like swelling at the end can be formed throughout the vegetation period. Their growth rate does not seem to follow any definite pattern and neither does the time of their origin. Generally, they begin to develop before or during flowering of the mother plant. One or two, exceptionally three, rhizomes per plant are formed. They grow horizontally (or, rather, parallel to the earth surface) and not very deep, only about 2-5 cm below the surface. The rhizomes are as a rule unbranched; only rarely one or two poorly developed lateral branches are produced. Rhizome length is obviously contingent upon both environmental and genetic factors: stout, vigorous plants do not necessarily produce long rhizomes and vice versa, with tiny speci-

Tab. 2: Representation (in %) in the topodemes examined of fertile and sterile shoots. — Anzahl der Blütensprosse bzw. sterilen Sprosse (in %) in den untersuchten Topodemen.

Topodeme no.	Fertile	Sterile
1	44	56
2	16	84
3	24	76
4	42	58
5	74	26
6	50	50
7	54	46
8	52	48
9	76	24

mens sometimes sprouting surprisingly long ones. While average rhizome length is about 30-50 cm, a normally developed plant with rhizomes only 1.5-4.0 cm long was found in topodeme no. 3 in late August when the aerial stem was already dying. The longest rhizomes (70-80 cm) can be produced both by robust plants (R form) and small ones (D form). The rhizomes are developed by all members of a population, both flowering and non-flowering, in a given year. A considerable proportion of the latter was observed in each of the topodemes studied. Plants producing no rhizomes were not observed.

The tuber-like terminal swelling on the rhizome is ellipsoid in the earliest stages of development; as rhizome growth proceeds, however, it soon assumes its characteristic mace-like shape, with a short hook at the distal end that gives rise to a new aerial shoot in the following spring. Blunt prickles start to elongate to produce roots in late summer, whereas the hook (with rudiments of leaves already discernible) becomes active in late winter and develops a new aerial shoot soon after the snow has melted in the following spring (Fig. 1). In warm autumns, rudiments of new rhizomes may be formed, but they do not produce any swellings. Thus, as noticed by HILDEBRAND (1876), three generations of a given plant can be seen at one moment: last year's stolon, the plant resulting from it, and the germ of next year's aerial shoot.

The capsule matures in July, its wall splitting into segments that become patent but remain connected to the fruit stalk. The aerial part of the mother plant starts to exhibit signs of senescence as early as late July and early August, the leaves first becoming pale yellow, then reddish-brown and finally light brown. It dies entirely in the course of September, whilst the subterranean organs continue to grow until late autumn, produce a new ramet (only one per rhizome or its branch), and the whole cycle is perpetuated. Consequently, *Trientalis europaea* grows into large clones that can penetrate one another and are responsible for the mosaic-like structure of the populations.

Thus, a considerable degree of mobility is gained and the location of the shoots in a given site may change considerably from one year to another. The same mode of reproduction has been observed in the related *T. borealis* RAFIN. (ANDERSON & LOUCKS 1973). Ramets living one year only are known to occur, e.g. in some *Allium* species (KAWANO & NAGAI 1975) — a case of pseudoannuals (URBANSKA 1992).

It is questionable, therefore, whether the subterranean organ of *Trientalis* can be described as a rhizome. A characteristic feature of rhizomes is that they last more than one growing season. In *Trientalis,* however, it is the subterranean system as a whole that survives (possibly for hundreds of years), whereas the rhizome as a morphological entity is renewed every year. Perhaps "annual rhizome" would better describe the situation.

A note on karyology

It follows from Table 3 that high ploidy levels are involved in all three species of *Trientalis* studied to date. No chromosome number information seems to be available for *T. latifolia* HOOK. In *T. europaea* L., the majority of counts are centered on or around 2n = 160, thus representing an extension of a polyploid series begun perhaps by *T. borealis* RAFIN. (2n = 96). The somatic number of 2n = 160 for *T. europaea* L. has been confirmed on material from the Czech Republic (topodeme no. 5; see Tab. 1).

Morphological variation

Table 4 shows that the normal form (N as defined by MEDWECKA-KORNAŚ) was by far the most frequent in all the topodemes studied. The diminutive form (D) proved to be only scattered, being present in all but two sites sampled. It was somewhat more numerous in the montane zone and above

Tab. 3: Chromosome numbers in *Trientalis*. — Chromosomenzahlen bei *Trientalis*.

Species	2n	References
T. europaea L.	c. 160	ROHWEDER 1937
	c. 160	WULF 1937
	112	LÖVE & LÖVE 1944
	c. 160	LÖVE 1954
	c. 160	LÖVE & LÖVE 1956
	> 100	SOKOLOVSKAYA 1960
	90	ZHUKOVA 1980
	90	ZHUKOVA 1982
	160	MURÍN & MÁJOVSKÝ in MÁJOVSKÝ & MURÍN 1987
T. borealis RAFIN.	96	LÖVE & LÖVE in LÖVE & SOLBRIG 1964
	96	LÖVE & LÖVE in LÖVE 1982
T. arctica FISCH.	c. 170	SOKOLOVSKAYA 1963
	90	ZHUKOVA & TIKHONOVA 1971

timberline in the Krkonoše and Hrubý Jeseník Mts. Individuals belonging to the ramose form (R) were represented, with varying frequency, in six sites. This is for the most part in agreement with the original concept by MEDWECKA-KORNAŚ (1963), who described — in material from Finland, Norway and Poland — N as a forest plant, D as having distinctly northern character, whereas the characterization of R is somewhat vague. She also noted that plants close to the diminutive form occur in the Rudohoří (= Krušné hory) Mts.

The number of leaves in a whorl "oscillates" on a rather limited scale, between 4 and 9, but their length "oscillates" over a wide range, the longest leaves occurring in some R plants (up to 69 mm long in topodeme no. 9). The leaves are invariably glabrous on both sides, tapering to the base, without a distinct petiole, and finely serrulate in the upper two thirds (Tab. 5, 6).

The number of alternate leaves varies from 0 to 5. They are rather irregularly spaced and may be stipular to foliar in shape, increasing in size from the base to the top of the stem. They are, however, always distinctly smaller than the leaves of the whorl, the transition between the uppermost leaf and the whorl being quite abrupt. Their number, shape and size do not appear to be correlated with those of the whorled leaves: an R plant may have only one rudimentary cauline leaf, whereas certain D plants display up to four well-developed alternate leaves (Tab. 5, 6).

There are 1-4 flowers per stem. Topodemes no. 1, 4, 5, 6 and 9 are shown to be predominantly uniflorous, while in the others, plants with two flowers prevailed. Triflorous plants are rare; four flowers showed up in two plants only, one from topodeme no. 7, the other from no. 9. All flowers normally arise from the leaf whorl, but occasionally the second and other flowers may originate from the axils of the uppermost alternate leaves (Tab. 5, 6, 7).

As indicated in Table 7, seven is the predominating number in the structure of the *Trientalis* flower, though hexamerous flowers are not at all rare. An enneamerous flower appeared only in topodeme no. 7, showing signs of developmental disturbances (calyx teeth irregularly spaced, corolla unevenly cleft). No pentamerous or decamerous flowers have been recorded (Tab. 5, 6, 7).

Tab. 4: Representation (in %) in the topodemes studied of the main growth forms (N = normal; D = diminutive; R = ramose; T = transitional). — Darstellung der Hauptwuchsformen (in %) in den untersuchten Topodemen (N = normal; D = diminutiv; R = verzweigt; T = Übergangsform).

Topodeme no.	N	D	R	T
1	90	-	-	10
2	52	12	12	24
3	52	24	6	18
4	78	-	-	22
5	68	2	6	24
6	76	6	6	12
7	62	10	8	20
8	44	24	4	28
9	96	2	-	2

Tab. 5: A summary of morphological variation in the topodemes examined: (1) = range of variation; (2) = average; (3) = standard deviation; (4) = standard error. Size of samples: 50. **A**: length of longest leaf in whorl (in mm). **B**: number of leaves in whorl. **C**: number of alternate leaves. **D**: number of flowers. **E**: number of floral parts. — Übersicht über die morphologische Variation der untersuchten Topodeme: (1) = Variationsbreite; (2) = Durchschnitt; (3) = Standardabweichung; (4) = Standardfehler. Probengröße: je 50. **A**: längstes Wirtelblatt (in mm). **B**: Anzahl der Wirtelblätter. **C**: Anzahl der wechselständigen Blätter. **D**: Blütenzahl. **E**: Anzahl der Blütenteile.

					Topodeme no.				
		1	2	3	4	5	6	7	8	9
A	(1)	26-65	18-56	21-45	28-64	23-67	23-63	22-61	22-62	22-69
	(2)	$44.5^{d,e}$	34.04^{b}	29.74^{a}	$41.10^{c,d}$	$42.38^{c,d}$	$43.58^{d,e}$	39.26^{e}	34.90^{b}	47.08^{e}
	(3)	10.34	9.39	6.88	8.49	9.82	4.63	8.66	6.86	10.58
	(4)	1.46	1.32	0.97	1.20	1.38	0.65	1.22	0.97	1.49
B	(1)	5-8	5-8	3-9	4-9	4-9	4-8	5-7	5-9	5-8
	(2)	6.32^{a}	$6.42^{a,b}$	$6.40^{a,b}$	6.22^{a}	$6.42^{a,b}$	6.04^{a}	$6.38^{a,b}$	6.76^{b}	6.06^{a}
	(3)	0.89	1.21	1.14	0.97	1.07	0.85	0.77	1.15	0.76
	(4)	0.13	0.17	0.16	0.13	0.15	0.12	0.11	0.16	0.10
C	(1)	0-3	0-3	1-5	0-4	0-4	0-3	0-5	1-4	0-4
	(2)	1.38^{a}	$2.06^{d,e}$	2.44^{f}	$1.64^{a,b}$	$2.12^{d,e}$	$1.92^{b,c,d}$	$1.76^{b,c}$	$2.32^{e,f}$	2.50^{f}
	(3)	0.56	0.73	0.90	0.82	0.77	0.72	0.84	0.89	0.73
	(4)	0.10	0.10	0.12	0.11	0.10	0.10	0.11	0.12	0.10
D	(1)	1-3	1-3	1-3	1-3	1-3	1-2	1-4	1-3	1-4
	(2)	$1.54^{b,c}$	$1.66^{c,d}$	$1.72^{c,d}$	1.20^{a}	$1.52^{b,c}$	$1.30^{a,b}$	$1.76^{c,d}$	1.84^{d}	$1.52^{b,c}$
	(3)	0.67	0.55	0.64	0.45	0.57	0.46	0.68	0.73	0.64
	(4)	0.09	0.07	0.09	0.06	0.08	0.06	0.09	0.10	0.90
E	(1)	6-8	6-8	6-7	6-7	6-7	6-8	7-9	6-8	6-8
	(2)	$6.94^{b,c}$	$6.94^{b,c}$	$6.92^{b,c}$	6.72^{a}	$6.86^{a,b}$	7.02^{c}	7.2^{d}	$6.92^{b,c}$	$6.92^{b,c}$
	(3)	0.31	0.42	0.27	0.45	1.07	0.42	0.45	0.44	0.34
	(4)	0.04	0.06	0.04	0.06	0.15	0.06	0.06	0.06	0.04

^{a,b,c} ... give results of multiple range analysis (95 % LSD intervals)

^{a,b,c} ... stellen die Ergebnisse der Multiple Range Analysis dar (95 % LSD-Intervalle)

Tab. 6: Analysis of variance (1) between groups, (2) within groups. Sample size: 450. **A**: length of longest leaf in whorl (in mm). **B**: number of leaves in whorl. **C**: number of alternate leaves. **D**: number of flowers. **E**: number of floral parts. — Varianzanalyse (1) zwischen den Gruppen, (2) innerhalb der Gruppen. Probengröße: 50 (je Gruppe). **A**: Länge des längsten Blattes im Wirtel (in mm). **B**: Anzahl der Blätter im Wirtel. **C**: Anzahl der wechselständigen Blätter. **D**: Anzahl der Blüten. **E**: Anzahl der Blütenteile.

		Sum of squares	Degrees of freedom	Mean square	F-ratio	Sign. level
A	(1)	128.05720	8	16.007150	18.892	0.0000
	(2)	373.66300	441	0.847308		
B	(1)	18.87111	8	2.358889	2.378	0.1620
	(2)	437.46000	441	0.991973		
C	(1)	56.99111	8	7.123889	11.06	0.0000
	(2)	283.90000	441	0.643764		
D	(1)	17.73778	8	2.217222	5.925	0.0000
	(2)	165.02000	441	0.374195		
E	(1)	6.49777	8	0.812222	5.286	0.0000
	(2)	67.76000	441	0.153651		

Tab. 7: Variation in the number of floral parts (in %) in the topodemes examined. — Variation in der Zahl der Blütenteile (in %) in den untersuchten Topodemen.

Topodeme no.	Hexamerous	Heptamerous	Octomerous	Enneamerous
1	8	90	2	-
2	12	82	6	-
3	8	92	-	-
4	28	72	-	-
5	14	86	-	-
6	8	82	10	-
7	-	82	16	2
8	14	80	6	-
9	12	86	2	-

Discussion

The phenotype of *Trientalis europaea* is considerably plastic, but, from the taxonomic viewpoint, this variation is negligible, having failed to produce any appreciable intraspecific units. For a polyploid species with such a vast geographical range, occurring in a variety of habitats (in Central Europe alone, from oak and oak-pine woodlands of the lowlands to subalpine peat bogs and *Pinus mugo* scrub), this is quite surprising and difficult to explain.

In a polyploid species consisting of both clones and plants that have presumably arisen sexually, one would expect a splitting into an array of more or less clean-cut taxa replacing each other geographically. Few, if any, intraspecific units described so far in *T. europaea* reflect the difficulty of partitioning largely continuous ranges of morphological variation into formally defined entities. What we see in *T. europaea* is rather a variation on a given theme.

This is most likely connected with the peculiar mode of reproduction, but apomicts, vegetative perhaps to a lesser degree than gametophytic, are known to produce endless series of morphologically recognizable entities which may or may not be amenable to taxonomic treatment. *T. europaea* is perhaps unique among apomicts in being taxonomically homogeneous throughout its geographical area.

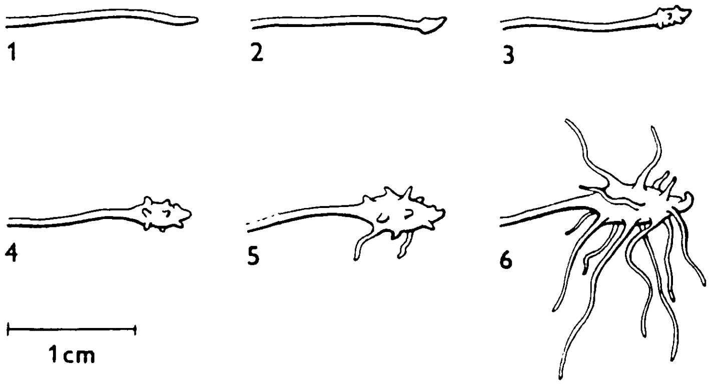

Fig. 1: The course of development from a simple swelling (1, 2) to a mature tuber (6). Note the hook at the distal end, which develops a new aerial shoot in the following spring. Drawing by A. SKOUMALOVÁ. — Der Entwicklungsvorgang von einer einfachen Verdickung (1, 2) zu einem vollentwickelten Rhizom (6). Zu beachten ist das distale Ende, das im darauffolgenden Frühjahr einen neuen Sproß bildet. Zeichnung: A. SKOUMALOVÁ.

It is tempting to speculate on the reasons for this condition. In the Primulaceae, base chromosome numbers vary greatly, but as far as polyploidy goes, the family is rather restrained, with polyploid series occurring, rather sporadically, only in *Primula* L., *Androsace* L., *Lysimachia* L., *Anagallis* L., *Cyclamen* L. and *Dodecatheon* L. and never attaining higher levels than tetraploid. *Trientalis* is aberrant in this respect. Autopolyploid origin (by repeated doubling of the initial diploid chromosome set) is unlikely: no recently evolved successful natural polyploid can be interpreted in such a way (STEBBINS 1959). Alloploidy is theoretically more plausible but would require hybridization of two "lesser-ploid" species. The obvious candidates, *T. borealis* RAFIN. and *T. arctica* FISCH., cannot be considered, being merely geographical races of *T. europaea* L. Perhaps two distinct species of *Trientalis* hybridized repeatedly, resulting in a repeated chromosome doubling, whereupon they became extinct. Their hybrid proved successful in terms of survival and geographical distribution. No heterosis set in, however: *T. europaea* plants are, compared with most of the Primulaceae, both diploid and tetraploid, definitely delicate. Obviously, as one goes beyond the tetraploid level, increases in chromosome number often result in abnormalities such as dwarfing and weak plants (STEBBINS 1950). This results from the genetic consequences of high polyploidy, and the degree of polyploidy at which imbalance sets in will depend upon the species or even the individual in question (SWANSON 1963). According to the latter author, "the doubling of an allotetraploid to give an octoploid individual would lead to a complex polyploid type having the characteristics of both auto- and alloploidy". It seems likely that a similar mechanism also operated and perhaps still operates in *T. europaea* L.

It is often argued that polyploidy runs concurrently with apomixis and is directly responsible for it. However, as pointed out by GUSTAFSSON (1946), while apomixis can be induced at diploid level by favourable gene combinations, there is a stronger action of these genes at the polyploid level; support for this contention can be derived from breeding experiments. Despite the high levels of polyploidy, there is no evidence of gametophytic apomixis in *Trientalis*. This is quite surprising because some phenomena concomitant with gametophytic apomixis are present, including the relative scarcity of sexual reproduction. However, vegetative apomixis is common and is largely responsible for the maintenance of *Trientalis* populations.

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