

Formal Report: Summary of Scientific Research Concerning *Trientalis borealis*.

Prepared for: Dr. Patrick Brown

Prepared by:

Date: November 21, 2011

Memorandum of Transmittal

To: Dr. Patrick Brown
Northern Michigan University Biology Department Head

From:
Northern Michigan University Biology Department

Date: November 21, 2011

Re: Formal Report Summarizing Research into *Trientalis borealis*

Upon your expression of interest in researching *T. borealis* I have composed a formal report summarizing the relevant scientific literature. The aim of this report is to detail the research I have done, and to make recommendations concerning the potential for *T. borealis* research.

It is my intention that this report sufficiently provide a foundation upon which you may decide to conduct research into *T. borealis*. However, if any questions, clarifications or recommendations concerning my research exist, please contact me at 616-252-9443.

Thank you for the opportunity to assist NMU's department of biology.

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ABSTRACT

Trientalis borealis is an herb found in boreal ecosystems of eastern North America. Furthermore, *T. borealis* is a clonal plant, and therefore displays biological and ecological characteristics which remain relatively un-researched. The main aim of this paper is to synthesize the major scientific works concerning *T. borealis*, and to articulate them in a broad, relatively nontechnical way. Research has primarily focused on 1) sexual reproduction, 2) asexual reproduction, and 3) population dynamics. However, many other aspects of clonal biology have also been researched and are therefore included in the synthesis. Indeed, *Trientalis borealis*' life cycle is generally well understood; including its seasonal growth, phenotypic range, and size and number of offspring. Less well understood, however, are, despite the abundance of research into these areas, the exact influences on reproduction and population dynamics. Likewise, the influences of temperature, light and habitat on reproduction have been researched, yet few conclusions exist.

In conclusion, I determine that further research into *T. borealis* is needed. Furthermore, research could proceed in variety of directions discussed in the report, for various ecological aspects remain open to investigation and interpretation.

INTRODUCTION

The northern starflower (*Trientalis borealis*) is a shade-tolerant clonal herb native to temperate mixed hardwood forests of North America. Most understory plants of mixed hardwood forests are clonal (Whigham 2004, p. 585), yet many aspects of *T. borealis*, as well as other clonal plants, remain un-researched and therefore unknown. Equally, many ecological aspects have been researched but require additional examination. The purpose of this paper is to summarize and articulate the central concepts of the scientific literature concerning *T. borealis*. My hope is that this synthesis will be useful to individuals interested in researching *T. borealis* or related clonal species.

An understanding of potential research concerning *T. borealis* is, however, impossible without a general knowledge of clonal plants; thus, an explanation of the nature of clonal plants and relevant terminology is first provided. Next, a phenotype and life history characterization details the specific biology of *T. borealis*.

Three central aspects of research are then discussed at length: 1) sexual reproduction via seed, 2) asexual reproduction via tubers, and 3) population dynamics. However, these areas of research are not mutually exclusive, and an intermingling of information necessarily exists.

METHODS

Scientific research published in peer reviewed journals composes the majority of information reviewed. Authors such as Roger Anderson and Jean Piqueras have written numerous papers on *T. borealis*, and their work is irreplaceable as a source of information. Additional authors (see Literature Cited) have also devoted their careers to researching clonal plants, and while all may not be directly interested in *T. borealis*, their research into similar clonal species nevertheless provides insight into *T. borealis*.

RESULTS

Clonal Plants

Scientific research which has attempted to understand the biology of *T. borealis* may be used to draw conclusions concerning other clonal species; conversely, research of other clonal plants may be extrapolated to *T. borealis*. Thus, a summarization of clonal biology allows a better understanding of *T. borealis*.

Clonal plants are capable of both sexual and asexual reproduction. Asexual reproduction entails vegetative growth, and “a single individual is the sole parent and passes copies of all its genes to its offspring” (Campbell et al. 2008, p. 249). Sexual reproduction requires the fusion of gametes, and a unique combination of genes is inherited by the offspring (Campbell et al. 2008, p. 249). As Robert Cook explains, in a clonal population ramets are the fundamental units which live, reproduce, and die, yet one genetic individual, a genet, is capable of surviving thousands of years (1983, p. 245). Ramets consist of the stem, leaves and roots, whereas a genet is the collective sum of many individual ramets derived asexually from a single parent. Paulette Bierzychudek writes that reproduction in clonal plants is dominantly asexual, whereas sexual reproduction via seed is rare (1982). *Trientalis borealis*, too, reproduces dominantly from propagules; a mother ramet produces 1 to 4 rhizomes (i.e. trailing underground roots) whose terminal end enlarges into a starchy tuber (Anderson 1983, p. 408). The next ‘generation’s’ ramet, then, develops from this tuber, and the previous year’s ‘generation’ senesces. However, in reality, the two ‘generations’ are genetically identical; in essence, the plant has only shifted its position not reproduced. Population increases only if multiple tubers are produced and survive.

In many clonal herbs both the mother and daughter ramets renew vegetative growth in the following season, or maintain a network of rhizomes capable of nutrient transfer between ramets

(Angevine et al. 1986). As Robert Cook clarifies, however, connections between ramets of *T. borealis* are degraded in the fall (1983, p. 245); thus, individual ramets are entirely independent, yet remain genetically identical to sister ramets of the surrounding genet. In species whose rhizomes maintain a connection, the identification of ramets into individuals is often arbitrary; it is unclear when a daughter ramet becomes physiologically independent (Cook 1983, p. 245). Furthermore, the study of asexual reproduction is rendered difficult in that underground rhizomes and tubers can only be observed by tediously uprooting them, yet Roger Anderson maintains that “the asexual propagules (tubers) are easily obtained” (Anderson 1983, p. 798).

***Trientalis borealis* Characterization**

Trientalis borealis is not unique in its clonal biology, and may therefore be used as a model organism to study clonal species. Nevertheless, a thorough characterization of *T. borealis*' phenotype and life history allows a stronger understanding of its ecology.

Phenotypic Description

Trientalis borealis is an herbaceous plant (i.e. a plant whose leaves and stem senesce annually). A whorl of 5 – 10 lance-shaped leaves (ca. 4 – 9 centimeters in length) form at the terminus of a 15 – 25 centimeter stalk (Chambers et al. 1996, p. 242). Brenda Chambers writes that flowers of 7 white petals develop from slender stalks (ca. 5 – 10 centimeters in length) projecting from the center of the leaf whorl, and the fruit of *T. borealis* is a small rounded capsule with numerous tiny, black seeds (1996, p. 242). As with any clonal herb, a significant portion of the plant is underground; indeed, tubers and rhizomes comprise 64.8% of the total dry weight of *T. borealis* (Anderson and Loucks 1973, p. 807). Dendritic (i.e. branching) roots arise from buds near the base of the plant (Chambers et al. 1996, p. 242), yet a specialized root, termed rhizome or stolon, comprises the majority of subterranean mass, for it produces at its

terminus a white tuber (ca. 2 – 10 cm in length and ca. 5 cm in diameter) (Anderson and Loucks 1973, p. 801). Plant size is, however, variable: Michael L Cain investigated the effects of habitat on plant size, yet found conclusive relationship. Cain also found that size of the mother ramet had little impact on rhizome production (1997). This contradicts Roger Anderson's earlier supposition of a link between a ramet's size and rhizome length (1973, p. 807). While size is easily observed, its exact determinants remain elusive to researchers.

Life History

The northern starflower is an understory herb in temperate mixed hardwood forests (Chambers et al. 1998, p. 242); the habitat range of *T. borealis* roughly equates that of the boreal forest and northern conifer-hardwoods in North American and is detailed in Figure 1 (Appendix A). *Trientalis borealis* has been termed a pseudo-annual by Jesus Piqueras, for individual ramets senesce each fall, however, an individual perennates (i.e. makes itself a perennial plant) by tuber formation (1998, p. 213). Therefore, individual ramets appear to die each year, yet genetically identical plants will arise from tubers the following spring; thus, the plant may be seen as an annual or a perennial. Regardless, Anderson argues that the life history of *T. borealis* can be broken into three distinct phases: vegetative development, rhizome growth, and tuber formation (1973, p. 807). An illustration of *T. borealis*' life history is presented in Figure 2 (Appendix A).

Vegetative Development

Vegetative growth begins in the spring as a new shoot develops from a tuber or, more rarely, from a seed. Elongation and vegetative growth continue until the ramet has reached a size of ca. 25 cm in height sometime in early summer (Chambers et al 1996, p. 242). Vegetative growth encompasses the development of flowers, also in early summer, and the simultaneous growth of roots (Anderson and Loucks 1973). Dennis Whigham argues that light is the most

important factor limiting the vegetative growth of woodland herbs (2004, p. 606). However, Michael Cain has found that other factors, including temperature and substrate, are equally important (Cain 1997). Roger Anderson researched the effects of temperature on growth, and discovered that *T. borealis* grows better in the cooler climates of their range. However, no definitive physiological or evolutionary explanation as to why exists (1973, p. 802-806). Undoubtedly each abiotic (i.e. non-living) property influences the growth of *T. borealis*, yet each factor's relative importance to growth is undetermined.

Rhizome Growth

The second phase of *T. borealis*'s life history is rhizome formation. A rhizome (i.e. an organ phenotypically resembling a root) is initiated at the base each ramet' stalk . Elongation of the rhizome continues into late summer (Anderson and Loucks 1973, p. 800-801). Rhizomes arise either as braches from a main rhizome or as individual projections from the ramet's stem (Anderson and Loucks 1973; Piqueras 1998). Rhizome length in *T. borealis* varied from 5 centimeters to more than 1 meter, with an average of 30 centimeters (Anderson 1983, p. 408). Mark Angevine found evidence suggesting habitat was a key determinant of the number of rhizomes produced (1986). Jesus Piqueras emphasized the importance of the mother ramet's size as a determinant of rhizome length (1998, p. 218), yet Michael Cain reports, "size [...] had little impact of rhizome production" (1997, p. 883). Furthermore, Cain researched the effects of light and habitat on rhizome production (i.e. the number of rhizomes produced by each plant), and found that "rhizome lengths were shorter in [...] high light, [and in] early successional forest[s]" (1997, p. 883). This relationship makes sense, for early successional forests have no developed canopy, and more light therefore reaches the herbaceous plants of the forest floor. Rhizome length and rhizome number have important implications for starflower's reproduction. However,

neither an explanation of the ultimate (i.e. evolutionary) causes of rhizome length or of rhizome number is present in the scientific literature.

Tuber Formation

Tuber formation is the physical pathway of asexual reproduction. In late summer the ends of rhizomes enlarge into a starchy tuber which develops premature leaves and incipient roots. However, the entire tuber, including developing leaves, remains underground until early spring (Anderson and Loucks 1973; Piqueras 1983, p. 215). Tuber enlargement continues in *T. borealis* until late fall whereupon the rhizome connecting the tuber and mother ramet is degraded (Anderson and Loucks 1973, p. 801-802); thus, by winter a physiologically independent tuber lays dormant beneath the soil.

Sexual Reproduction

Importance

Only 2% of *T. borealis*' dry weight was apportioned to sexual reproduction (Anderson and Loucks 1973, p. 808), indicating sexual reproduction's low importance. Indeed, seed germination is so rare that Dr. Alan Rebertus maintains that it has never been observed in the wild (Personal Interview). The phenomenon of rare seedling establishment is common among clonal plants (Galen et al. 1985). Roger Anderson argued in his paper attempting to determine sexual reproduction's role in the ecology of *T. borealis* that "ecological studies of individual species have as a primary objective the evaluation and analysis of species adaptations to their environment" (1973, p. 798). As the benefits of sexual reproduction are numerous, the question of what evolutionary adaptations have restricted sexual reproduction in *T. borealis* must be researched further.

Cross-pollination

Roger Anderson found that northern starflower's flowers have a high degree of self-incompatibility (i.e. fertilization of a flower's ovary by pollen from the same genet produces unviable seeds) (1983, p. 413). Yet, Anderson maintains that no insects have ever been observed visiting *T. borealis*' flowers (1973, p. 802). Without insects cross pollination is relatively rare, especially considering the clonal nature of *T. borealis*: all of the individuals in a particular area are of one genet, and insects are therefore needed to disperse pollen if selfing (i.e. a plant fertilizing itself, or two ramets of the same genet fertilizing each other) is to be avoided. Without cross pollination no increase in genetic variability occurs, and populations of *T. borealis* are therefore more susceptible to environmental change (Campbell et al. 2008, p. 1248).

Environmental Effects on Seedling Germination

The role of temperature in seedling establishment was researched by Roger Anderson, yet no significant relationship was found (1983). Northern Michigan University biologist Alan Rebertus has also investigated seedling establishment in *T. borealis*. He proposed that fire may be necessary for germination, yet after experimentation no seed germination was induced by fire (Personal Interview). While science does not understand the role of seeds in *T. borealis*'s life history, they are nevertheless produced, indicating a need to investigate the evolutionary role of seeds in clonal species, and the environmental effects acting upon seedling establishment.

Asexual Reproduction

Importance

A genet can achieve a life span of hundreds or even thousands of years (Cook 1983), yet, as ramets senesce annually, vegetative reproduction is necessary if the genet is to survive. Mathematically, two or more tubers, each surviving to become an individual plant, must be

produced to increase the population size. Indeed, an allocation of 64.8% of total dry weight in *T. borealis* was appropriated to tubers and rhizomes (Anderson and Loucks 1973, p. 807). Jesus Piqueras and Mark Angevine both investigated the life cycles of clonal plants to determine any patterns in their vegetative reproduction. It was found that the production of a daughter ramet whose size was equal to or greater than that of the mother ramet was most important to genet survival (1983; 1986). This confirms the view that asexual reproduction is a mechanism of ramet replacement in *T. borealis*. Indeed, 70% of *T. borealis* plants studied by Piqueras produced only 1 tuber for perennation (1983, p. 220). Anderson observed a similar result: 61.3% of plants produced 1 tuber and 30% produced 2 tubers (1973, p. 801), indicating that most ramets are preoccupied with replacement, and only a minority of ramets produce enough tubers to grow the population.

Environmental Effects on Asexual Reproduction

A negative correlation was found to exist between the number of tubers produced and their size (i.e. more tubers resulted in a smaller mean tuber size) by Anderson (1983). Furthermore, Piqueras found that the survival of daughter ramets showed a positive correlation to size; an increase in tuber size related to an increase in survival (1998, p. 220); thus, a ramet producing more tubers decreases each tuber's survival probability. Additional tubers are, however, required to grow the population, suggesting a life history tradeoff between number and size/survival rate. Furthermore, Jesus Piqueras suggests that the survival rates of the smallest tubers (i.e. tubers from ramets producing multiple tubers) had the most significant impact on population dynamics (1998, p. 220).

The effect of temperature and day length on tuber formation was studied by Roger Anderson: longer day length correlated to higher asexual reproduction biomass, a majority of the

biomass being composed of rhizome; whereas shorter day length and colder temperatures produced a larger allocation of resources to tubers (1970, p. 122). Thus, geographically northern ramets produced larger tubers. This has important consequences on survival (i.e. larger tubers survive more readily), and has consequences on the population dynamics, particularly the range of *T. borealis*.

Population Dynamics

Demography is a central theme of research concerning *T. borealis*. As Mark Angevine explains, “of [...] population processes in clonal plants [...] population dynamics has received the most attention” (1986, p. 548). However, population dynamics may also be the least understood aspect of clonal plants. Michael Cain emphasizes that “it remains a central challenge in biology to understand factors that govern the long-term dynamics of plant populations” (1983, p. 883). Two aspects of population dynamics have nevertheless been clarified. First, Ove Erickson demonstrated the significance of mobility in clonal plants as a mechanism of escape from competition to superior habitat (1988). Thus, competition may be affecting population movement. Indeed, entire genets are capable of moving, for if individual ramets grow rhizomes in a prevailing direction, then the entire genet will eventually move its position. Second, Roger Anderson demonstrated that day length was important to tuber size, and suggests that the southern populations of *T. borealis* may be limited by environment (1970, p. 122). However, the main influences on the population dynamics of *T. borealis* remain unknown.

DISCUSSION

A well-developed foundation of knowledge of *T. borealis*' biology is available to support research of *T. borealis* and of other clonal plants. However, the environmental influences affecting the size of ramets, genets, rhizomes, and tubers is not well understood. The relative

roles of sexual and asexual production are well researched and well understood, however, reproduction's influence on population and evolutionary viability requires further research, for few conclusions concerning reproduction's role in *T. borealis* exist. It appears that temperature and light are the main factors influencing population dynamics, yet the importance of each as well as the importance of additional abiotic influences on reproduction and phenotypic of *T. borealis* is not understood. Overall, population dynamics of *T. borealis*, and clonal plants as an entirety, are largely ambiguous. For example, the effects of the environment on population size and distribution are absent from the scientific literature concerning *T. borealis*.

RECOMMENDATIONS

Further research into *T. borealis* is necessary and should be pursued. Research may concentrate on sexual reproduction, asexual reproduction, population dynamics, or an additional ecological topic reviewed. However, if research is to be conducted, then it is critical that the appropriate literature is reviewed in more detail, for this paper only synthesizes the main points, and much is omitted. In conclusion, much has been written concerning *T. borealis*' ecology, yet additional research and thought is needed to complete our understanding of clonal ecology.

LITERATURE CITED

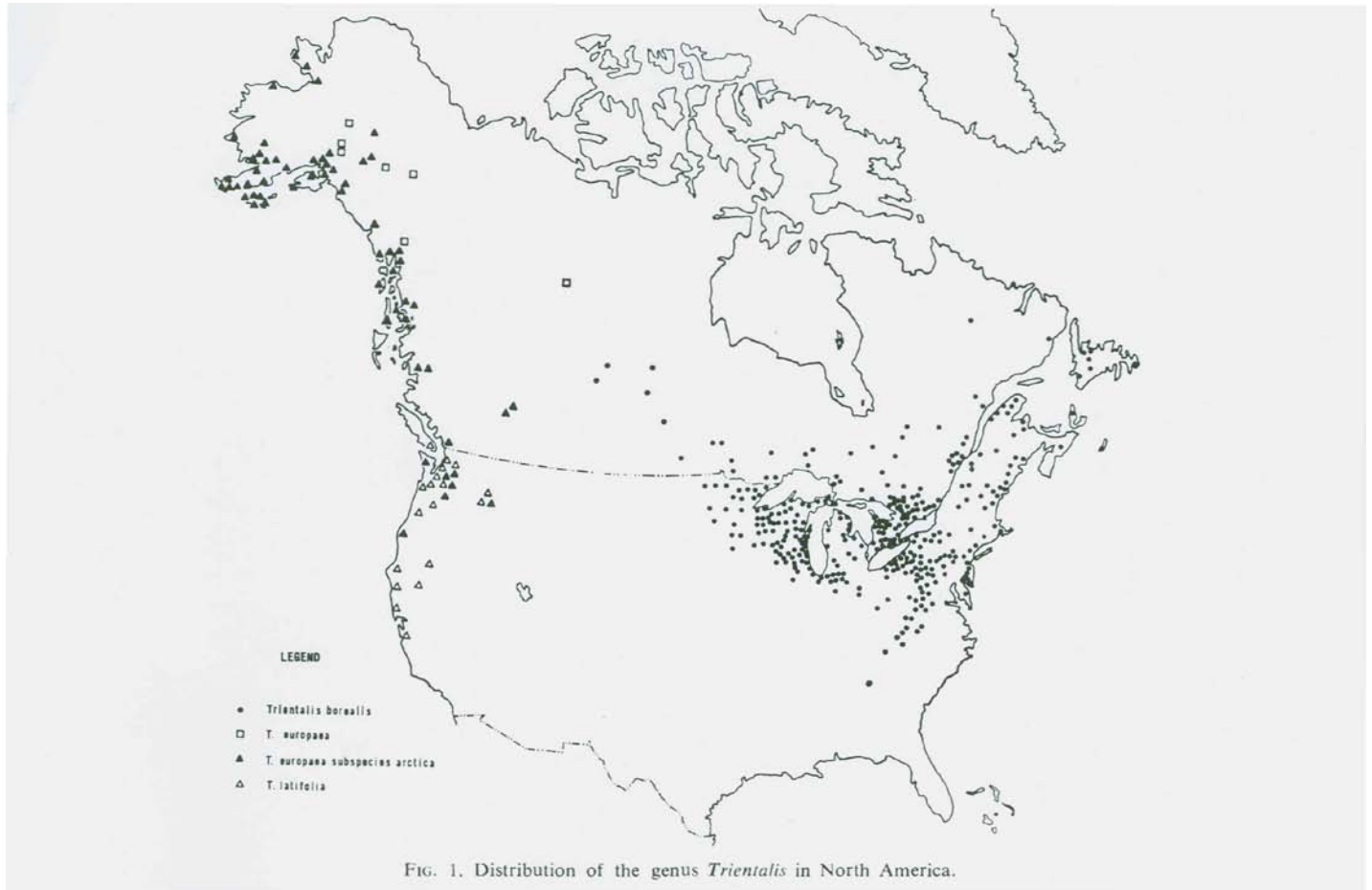
- Anderson, R. C. 1970. The role of daylength and temperature in tuber formation and rhizome growth of *Trientalis borealis*. Bot. Gaz. 131(2): 122-128.
- Anderson, R. C., and M. H. Beare. 1983. Breeding systems and pollination ecology of *Trientalis borealis* (Primulaceae). Amer. J. Bot. 70(3): 408-415.
- Anderson, R. C., and O. L. Loucks. 1973. Aspects of the biology of *Trientalis borealis* Raf. J. of Ecology. 54(3): 798-808.
- Angevine M. W., and S. N. Handel. 1986. Invasion of forest floor space, clonal architecture, and population growth in the perennial herb *Clintonia borealis*. J. of Ecology. 74: 547-560.
- Bierzychudek, Paullete. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytol. 90: 757-776.
- Cain, M. L. and H. Damman. 1997. Clonal growth and ramet performance in the woodland herb, *Asarum canadense*. J. of Ecology. 85: 883-897.
- Campbell, Neil A. et al. *Biology*. 8th ed. Vol. 1. San Francisco: Pearson Benjamin Cummings, 2008. Print.
- Chambers, B., K. Legasy, and C. V. Bentley. Forest Plants of Central Ontario. Alberta, CA: Lone Pine Publishing, 1998. Print.
- Cook, R. E. 1983. Clonal plant populations: a knowledge of clonal structure can affect the interpretation of data in a broad range of ecological and evolutionary studies. American Scientist. 71: 244-253.
- Dr. Alan Rebertus. Personal interview. 25 October 2011.
- Eriksson, O. 1988. Patterns of ramet survivorship in clonal fragments of the stoloniferous plant *Potentilla anserina*. Ecology. 69(3): 736-740.

- Galen, C., R. C. Plowright, and J. D. Thomson. 1985. Floral biology and regulation of seed set and seed size in the lily, *Clintonia borealis*. *Amer. J. Bot.* 72(10): 1544-1552.
- Piqueras, J., and L. Klimes. 1998. Demography and modeling of clonal fragments in the pseudoannual plant *Trientalis europaea* L. *J. of Plant Ecology.* 136: 213-227.
- “Plants Profile for *Trientalis borealis*; Starflower.” *United States Department of Agriculture.* United States Government, n.d. Web. 8 Nov. 2011. <<http://plants.usda.gov/java/profile?symbol=TRBO2>>.
- "Starflower (*Trientalis borealis*)." *Connecticut Wildflowers.* Connecticut Botanical Society, 2005. Web. 14 Nov. 2011. <<http://www.ct-botanical-society.org/galleries/trientalisbore.html>>.
- Whigham, D. F. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol. Evol. Syst.* 35: 583-621.

APPENDIX A

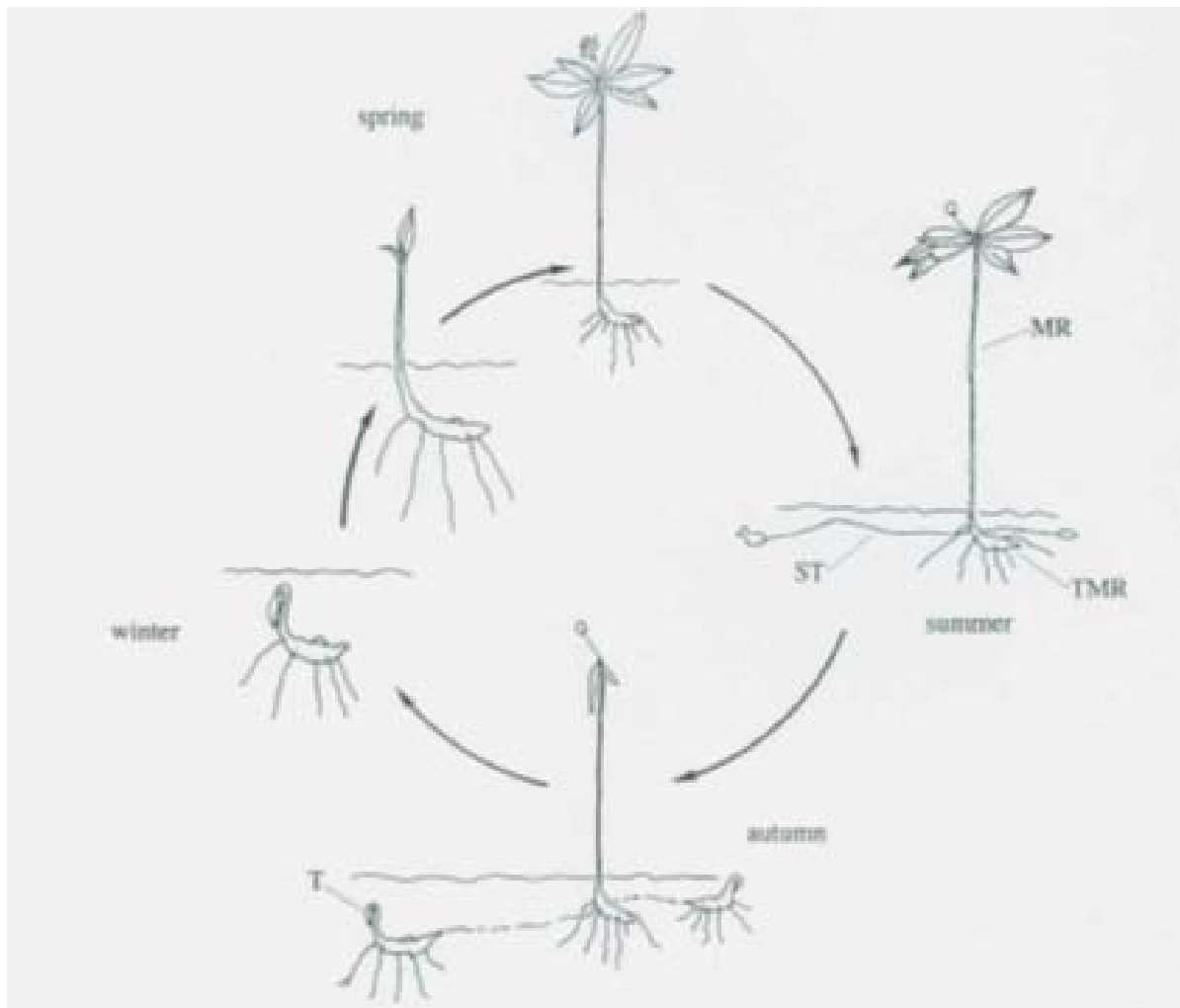
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Figure 2, Life Cycle of <i>Trientalis borealis</i>	16

Figure 1. Habitat distribution of *Trientalis borealis*. Figure 1 displays the habitat distribution of *Trientalis latifolia* (open triangles), *Trientalis europea* (open squares), *Trientalis europea* var. *artica* (black triangles), and *Trientalis borealis* (black circles). *Trientalis borealis* inhabits primarily eastern North America, including much of the Appalachian Mountains and the region surrounding the great lakes.



Source: Anderson and Loucks 1973.

Figure 2. Life cycle of *Trientalis borealis*. Figure 2 details the life cycle of *Trientalis borealis* from the formation of a tuber in autumn to vegetative growth and subsequent reproduction.



Source: Piqueras 1998.