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ORIGINAL PAPER

Ontogeny influences developmental physiology of post-transplant *Quercus rubra* seedlings more than genotype

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Abstract

• ***Key message*** **Seedling ontogeny exerted a greater influence on physiological activity of *Quercus rubra* seedlings than genetics; thus, it may be more important to use an appropriate growth index to account for seedling ontogeny in experiments than to control for genetic variation.**

• ***Context*** Members of the genus *Quercus* exhibit semi-determinate growth, resulting in complex and developmentally variable endogenous physiological patterns. The *Quercus* morphological index (QMI; Hanson et al. Tree Physiol. 2:273-281, 1986) was developed as a tool to relate physiological patterns to morphologically identifiable ontological stages, thereby allowing for treatment or measurement of seedlings at uniform ontological stages rather than strictly by chronology.

• ***Aims*** Although clear physiological patterns relative to seedling ontogeny have been observed using the QMI in pre-transplant half-sibling seedlings, we sought to determine whether physiological patterns remain consistent across genotypes within a species.

• ***Methods*** We examined net photosynthesis, transpiration, leaf chlorophyll concentrations, and chlorophyll fluorescence (F_v/F_m) throughout the first flush after transplant for northern red oak (*Quercus rubra* L.) seedlings from three half-sibling families.

• ***Results*** Neither net photosynthesis nor transpiration rates varied by family, whereas leaf chlorophyll concentrations and F_v/F_m differed significantly. Despite family differences for magnitudes of some parameters, no interactions between QMI growth stage and family were observed, and patterns of all parameters relative to growth stage were consistent across families. Net photosynthetic rates, transpiration rates, and F_v/F_m increased during the flush, while leaf chlorophyll concentration decreased, suggesting that chlorophyll synthesis is not a limiting factor during leaf maturation in this species.

• ***Conclusion*** Findings indicate that QMI-based physiological patterns may be at least regionally applicable within a given *Quercus* species.

Keywords Growth index · Episodic growth · Plant development · Seedling physiology · Experimental error

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Contribution of the co-authors JLS designed and conducted the experiment, analyzed the data, and co-wrote the manuscript. DFJ supervised the work and co-wrote the manuscript.

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1 Introduction

Species in the genus *Quercus* exhibit semi-determinate growth patterns, frequently characterized by recurrent flushes within a growing season resulting in complex endogenous physiological patterns relative to many co-occurring species with determinate or indeterminate growth patterns (Hanson et al. 1986; Dickson et al. 2000a, b). The *Quercus* morphological index (QMI) was developed by Hanson et al. (1986) as a growth index for physiological studies in this genus and has been used to identify ontological, rather than chronological, periods of seedling development. Thus, the QMI makes it possible to perform experimental treatments or measurements at particular ontological stages and states of physiological

activity, thereby reducing experimental error resulting from the use of seedlings of various developmental stages in physiology studies (Hanson et al. 1986; Dickson et al. 2000a, b). The use of the QMI in seedling physiology studies and, consequently, the validity of findings from these studies depend on the assumption that all *Quercus* seedlings of a given species and ontological stage exhibit similar physiological patterns; however, this assumption has not previously been explicitly examined.

The existence and importance of intraspecific variation is acknowledged by such practices as common garden studies and the establishment of seed zones, and high levels of intraspecific variation have been found for both European and North American oak species (Kleinschmit 1993; Kriebel 1993). However, detailed studies to characterize the extent and nature of endogenous physiological variability within a species in relation to specific ontological events, especially studies investigating members of the genus *Quercus*, are relatively few. The questions to be answered in this regard are twofold. First, does physiological activity in relation to discrete morphologically identified indicators of seedling ontogeny vary appreciably among family groups within a species and, if so, to what extent? Second, if substantial variability among family groups occurs at comparable growth stages, to what extent does it result from similar patterns of physiological activity throughout the species (differing primarily in the magnitude of activity) as opposed to the presence of multiple, inherently different patterns of endogenous physiological activity? Such questions of variation must be understood to make informed inferences as to whether results of any given isolated research experiment (often involving individuals that are relatively homogeneous genetically) are likely to apply to a species as a whole. Issues of intraspecific variation influence the applicability of research findings; for example, the vast majority of temperate deciduous hardwood seedlings produced for outplanting in the eastern USA, including most northern red oak seedlings, originate from genetically unimproved materials (Jacobs and Davis 2005), implying high degrees of intraspecific variation and poor predictability of seedling performance.

Many instances of intraspecific variation (both morphological and physiological) are regional in nature, often linked to environmental conditions, such as changing precipitation or temperature regimes throughout the range of a species. In cork oak (*Quercus suber* L.), a common garden study using acorns collected from throughout the species range found variation in leaf size, specific leaf area, and carbon isotope discrimination corresponding to rainfall and temperature differences between the seed sources (Ramírez-Valiente et al. 2010). Another common garden study examining intraspecific variation in white ash (*Fraxinus americana* L.) involving representatives from populations throughout the native range also linked variability in survival, diameter growth, leaf mass and nitrogen per unit area, and carbon isotope discrimination to differences in precipitation between geographic points of origin; however, the same study found no evidence of significant variation in light-saturated photosynthesis or stomatal conductance between populations (Marchin et al. 2008). Similarly, in red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* (Mill.) B.S.P.), regional intraspecific variation was observed in such parameters as germination time, hypocotyl height, epicotyl height, and total cotyledon area (Major et al. 2003).

In other instances, intraspecific variation occurs within a relatively small and homogenous geographical area, does not seem to result from adaptation to any obvious environmental factors, and appears to be a reflection of inherently diverse physiological patterns within a species. A study of intra- and interspecific genetic variability within and among several populations of white oak (*Quercus alba* L.), swamp white oak (*Quercus bicolor* Willd.), and bur oak (*Quercus macrocarpa* Michx.) in northeastern Illinois, USA, found not only the expected interspecific variability but also highly significant intraspecific genetic differentiation within each species examined; intraspecific variation was comparable to observed levels of interspecific variability (Craft and Ashley 2006). However, analysis of variation in chloroplast DNA of northern red oak (*Quercus rubra* L.) populations in Indiana, USA, found that individuals of different geographic populations varied more than individuals within populations (Romero-Severson et al. 2003).

Studies of intraspecific variation within European species of the genus *Quercus* have revealed similar variability. A study of monoterpene emissions of holm oak (*Quercus ilex* L.) found that the species contains no fewer than three distinct chemotypes, each with a characteristic monoterpene emission profile; although magnitude of these emissions varied seasonally, composition of the emissions was found to be inherently, consistently, and qualitatively different among chemotypes within the species (Staudt et al. 2001). Additionally, a study of the responses of sessile oak (*Quercus petraea* (Mattuschka) Liebl.) and English oak (*Quercus robur* L.) to flooding, using seedlings grown from acorns collected from a limited geographical area within a single forest, found substantial variability both between and within species, as well as the occurrence of individuals exhibiting extreme phenotypes for parameters such as density of induced hypertrophied lenticels, adventitious root number, and adventitious root biomass (Parelle et al. 2007).

The literature suggests that levels of intraspecific variation can differ substantially between species within a given genus and, consequently, should be assessed for each species, as experimental needs require. Studies employing the QMI assume the relation of physiological patterns relative to morphologically identified ontological stages remains consistent within a given species, although this assumption is rarely overtly examined or discussed and remains questionable for most

members of the genus. This study was initiated to determine whether northern red oak seedlings of different open-pollinated half-sibling groups exhibit similar post-transplant physiological patterns with regard to QMI growth stages and whether findings of studies of northern red oak employing the QMI can be expected to apply regionally within the species. To this end, regional intraspecific variation exhibited in patterns of gas exchange, chlorophyll fluorescence, and leaf chlorophyll concentrations during the first flush of growth following transplanting were evaluated.

2 Materials and methods

2.1 Plant material and transplant

Seedlings were grown from acorns collected in fall 2005 from three open-pollinated northern red oak mother trees representative of two populations within the state of Indiana (designated families 47, 49, and 97) located in a seed orchard at the Indiana Department of Natural Resources nursery near Vallonia, Indiana, USA (38° 48′ N, 86° 06′ W). This seed orchard contains mother trees established from scion wood collected from dominant northern red oak trees from around the state, with families 47 and 49 originating from Carroll County, Indiana, and family 97 originating from Allen County, Indiana. Acorns collected from the mother trees representative of these families in the seed orchard were sown in beds at the nursery and grown according to standard nursery production methods (Jacobs 2003) during the 2006 growing season; the dormant seedlings were operationally lifted in late fall and stored at 3 °C until April 2007.

In April of 2007, 24 seedlings from each half-sibling group were removed from cold storage for transplanting. Each seedling of each half-sibling group was randomly assigned a QMI growth stage (defined below) for physiological measurements and harvest, planted in 6.23 l pots (TPOT2, Stuewe & Sons, Inc.; Tangent, OR, USA) containing a 1:1 (*v*:*v*) mixture of sand and sphagnum peat, watered to container capacity (determined gravimetrically at time of transplant), and placed on benches in a climate-controlled greenhouse in the Department of Horticulture and Landscape Architecture greenhouse facility at Purdue University in West Lafayette, IN, USA (40° 25′ N, 86° 55′ W) under ambient light and day length with day/night temperatures of 24/20 °C. Seedlings were watered to container capacity daily throughout the study period, and greenhouse conditions were chosen so as to provide non-limiting growth conditions favorable to this species.

2.2 Regular morphological measurements

Quercus morphological index growth stages for physiological measurements and harvest were identified by a series of regular morphological measurements as described by Hanson et al. (1986). The linear shoot growth stage (SL) was indicated by cessation of elongation of the first new internode of the flush, the linear leaf growth stage (LL) by cessation of elongation of the shoot as a whole, and the lag stage (LAG) by cessation of elongation of the second leaf from the top of the new flush.

2.3 Physiological measurements

Physiological measurements were conducted on each seedling at its assigned growth stage. Measurements included net photosynthesis, transpiration, leaf chlorophyll concentration, and the ratio of variable fluorescence to maximal fluorescence in a dark-acclimated leaf (F_v/F_m). All measurements were performed on the same leaf.

Net photosynthesis was measured on mid-flush, sun-exposed leaves from 16:00 to 17:00 using an LI-6400 portable photosynthesis system equipped with a 6400-02B LED light source on a 2 × 3 cm broadleaf sampling head (Licor; Lincoln, NE, USA). Its settings were as follows: block temperature = 25 °C, photosynthetically active radiation (PAR) = 350 μmol m^{-2} s^{-1}, reference CO_2 = 400 μmol mol^{-1}, and flow rate = 400 mmol s^{-1}. At 23:30, F_v/F_m measurements were performed using an LI-6400 equipped with a 6400-40 leaf chamber fluorometer (Licor; Lincoln, NE, USA); measurement at this time ensured that seedlings experienced a minimum of 2 h of darkness to facilitate dark-acclimation of the leaves prior to measurement. Machine settings were the same as above, with light source and leaf chamber fluorometer settings adjusted as recommended in the user manual for F_v/F_m measurements.

Following chlorophyll fluorescence measurements, the leaf was removed, 10 leaf punches (8 mm diameter) were taken, chlorophyll extractions were immediately performed, and chlorophyll *a* and *b* concentrations were quantified spectrophotometrically (Arnon 1949; Hiscox and Israelstam 1979).

2.4 Statistical analyses

Data were analyzed as a completely randomized 3 × 3 factorial design (n = 8 seedlings for each family × growth stage combination with one leaf measured per seedling) using analysis of variance ($P < 0.05$) followed by Tukey's multiple pairwise comparison ($\alpha = 0.05$) to identify significant differences between families and growth stages. All analyses were performed using SAS software version 9.4 (SAS Institute, Inc., Cary, NC, USA).

3 Results

3.1 Photosynthesis

No interaction occurred between family and growth stage for net photosynthesis ($P = 0.28$). No difference in rates of net photosynthesis was observed between families over the course of the experiment ($P = 0.12$). Growth stage affected rates of net photosynthesis ($P < 0.01$), with higher rates of net photosynthesis occurring at LAG stage than at either the SL or LL stages (Fig. 1).

3.2 Transpiration

No interaction occurred between family and growth stage for transpiration ($P = 0.57$). No difference in transpiration rates was observed between families over the course of the experiment ($P = 0.11$). Growth stage, however, did have an effect ($P = 0.01$), with higher transpiration rates during LAG stage relative to the SL growth stage (Fig. 2).

3.3 Chlorophyll concentration

No interaction between family and growth stage was observed for chlorophyll *a* concentration ($P = 0.48$). A family effect was observed ($P = 0.01$), with family 47 exhibiting a higher chlorophyll *a* concentration (0.0067 ± 0.0017 mg chlorophyll *a* per 100 mg fresh mass) relative to family 49 (0.0056 ± 0.0016 mg chlorophyll *a* per 100 mg fresh mass). Additionally, a growth-stage effect was observed ($P < 0.01$), with LAG stage having a lower chlorophyll *a* concentration (0.0044 ± 0.0009 mg chlorophyll *a* per 100 mg fresh mass) relative to the SL or LL growth stages (0.0073 ± 0.0012 mg chlorophyll *a* per 100 mg fresh mass and 0.0066 ± 0.0012 mg chlorophyll *a* per 100 mg fresh mass, respectively).

With regard to chlorophyll *b* concentration, no interaction between family and growth stage was observed ($P = 0.56$), and no family effect was observed ($P = 0.17$). However, a growth-stage effect was observed ($P < 0.01$), with LAG stage having a lower chlorophyll *b* concentration (0.0118 ± 0.0024 mg chlorophyll *b* per 100 mg fresh mass) relative to the SL or LL growth stages (0.0176 ± 0.0028 mg chlorophyll *b* per 100 mg fresh mass and 0.0165 ± 0.0025 mg chlorophyll *b* per 100 mg fresh mass, respectively).

For total chlorophyll concentration, no interaction between family and growth stage was observed ($P = 0.54$), and no family effect was observed ($P = 0.07$). However, a growth-stage effect was observed ($P < 0.01$), with LAG stage having a lower total chlorophyll concentration (0.0162 ± 0.0033 mg total chlorophyll per 100 mg fresh mass) relative to the SL or LL growth stages (0.0250 ± 0.0039 mg total chlorophyll per 100 mg fresh mass and 0.0231 ± 0.0034 mg total chlorophyll per 100 mg fresh mass, respectively; Fig. 3).

3.4 Chlorophyll fluorescence

No interaction occurred between family and growth stage with regard to F_v/F_m ($P = 0.38$). A family effect was observed ($P < 0.01$), with family 47 having a reduced F_v/F_m value relative to families 49 and 97. Additionally, a growth-stage

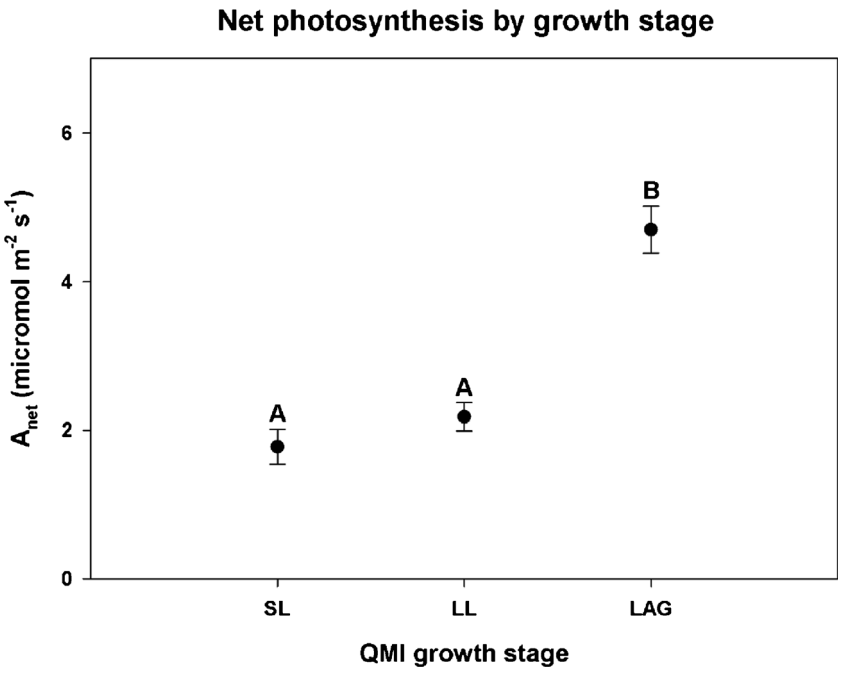

Fig. 1 Net photosynthesis by growth stage. Values displayed are means (± standard error of the mean), where $n = 24$ for each growth stage. Growth stages are shoot linear (*SL*), leaf linear (*LL*), and lag (*LAG*); stages marked with the *same letter* did not differ significantly ($\alpha = 0.05$)

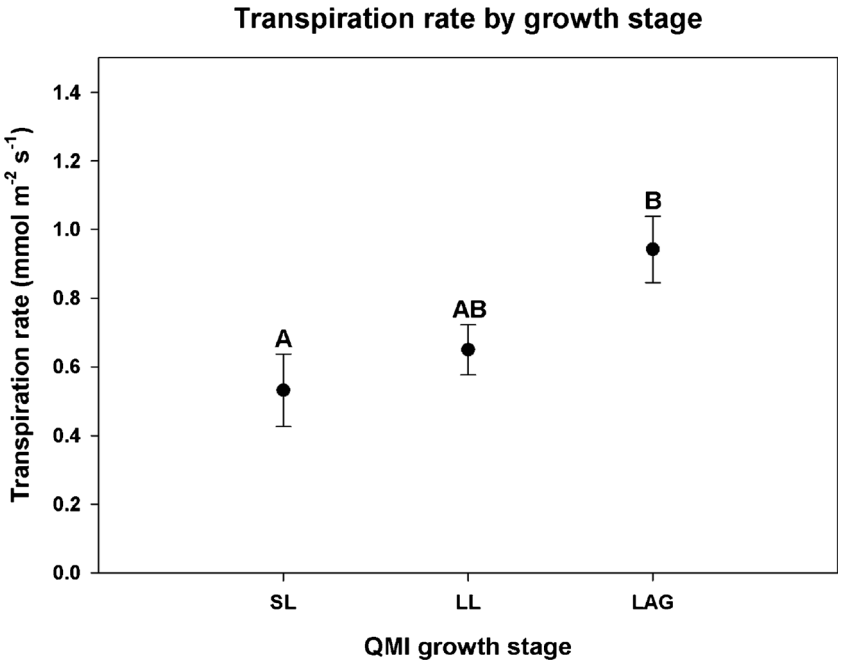

Fig. 2 Transpiration rate by growth stage. Values displayed are means (± standard error of the mean), where $n = 24$ for each growth stage. Growth stages are shoot linear (*SL*), leaf linear (*LL*), and lag (*LAG*); stages marked with the *same letter* did not differ significantly ($\alpha = 0.05$)

effect was observed ($P = 0.01$), with LAG stage having a higher F_v/F_m value relative to the SL growth stage (Fig. 4).

4 Discussion

Minimal intraspecific variation was observed among the three half-sibling groups of northern red oak used in the experiment, and in no case did the underlying ontological patterns exhibited by net photosynthetic rate, transpiration rate, leaf total chlorophyll concentration, or chlorophyll fluorescence appear to vary by family group. The apparent absence of intraspecific variation in patterns of physiological activity relative to growth stage is supported by the lack of interaction between the growth stage and family group factors for all measured parameters. The low variability among family groups in the present study contrasts with high levels of intraspecific variation observed in studies with other *Quercus* species (Staudt et al. 2001; Craft and Ashley 2006; Ramírez-

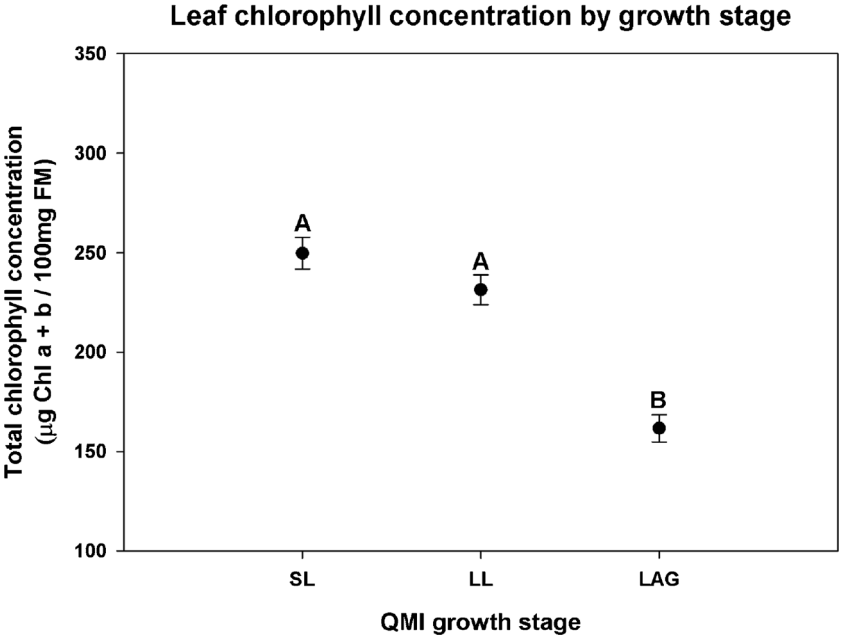

Fig. 3 Leaf chlorophyll concentration by growth stage. Values displayed are means (± standard error of the mean), where $n = 24$ for each growth stage. Growth stages are shoot linear (*SL*), leaf linear (*LL*), and lag (*LAG*); stages marked with the *same letter* did not differ significantly ($\alpha = 0.05$)

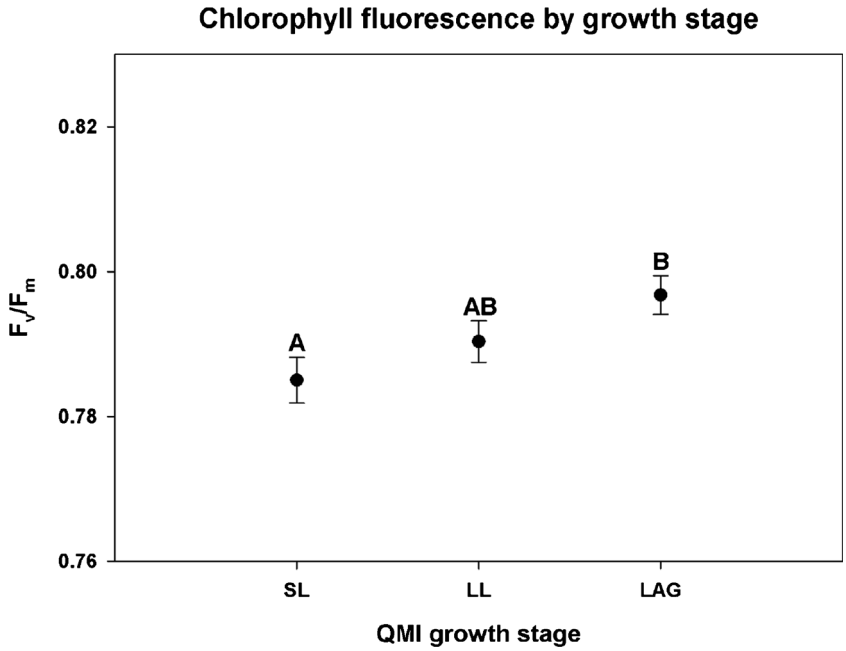

Fig. 4 Chlorophyll fluorescence by growth stage. Values displayed are means (± standard error of the mean), where $n = 24$ for each growth stage. Growth stages are shoot linear (*SL*), leaf linear (*LL*), and lag (*LAG*); stages marked with the *same letter* did not differ significantly ($\alpha = 0.05$)

Valiente et al. 2010); however, it should be noted that all three families used originated from within Indiana, USA, and therefore may not be fully representative of variation within this species across its range. Growth stage exerted much greater influence on the magnitudes and patterns of physiological activity in post-transplant seedlings than family group, further highlighting the importance of using a growth index in physiological research of *Quercus* spp. In principle, the findings of this study also support the potential for broad applicability within any species of research findings based upon a morphological index appropriate to that species.

Somewhat surprisingly, neither net photosynthetic rates nor transpiration rates varied by family; however, growth stage had a large effect on both net photosynthesis and transpiration (Figs. 1 and 2, respectively), with both parameters increasing steadily throughout the flush until LAG stage when the experiment was concluded. Isebrands et al. (1994) observed patterns of steadily increasing net photosynthetic rates during leaf expansion and development in pre-transplant northern red oak seedlings during the course of the first flush of growth following germination and again in second-flush leaves; the present study finds these patterns to occur similarly in post-transplant seedlings, remaining consistent across the family groups examined.

Chlorophyll *a*, chlorophyll *b*, and total chlorophyll concentration responses to growth stage were very similar across families, suggesting that patterns of chlorophyll synthesis occur with ontological consistency across genotypes for northern red oak seedlings. Growth stage heavily influenced these same parameters, with steep declines in mass-based concentrations of each observed at LAG stage (Fig. 3). Such a pattern is suggestive of the growth dilution of chlorophyll during leaf expansion over the course of the flush, and, considering the relatively low levels of current photosynthate partitioned into pigments following the completion of leaf expansion observed by Dickson et al. (2000b), the present data suggest that chlorophyll synthesis is largely completed by the SL growth stage of the flush. Additionally, the observed inverse relation between net photosynthetic rates and leaf chlorophyll concentrations suggests that increases in carbon exchange rates of new leaves, which continue to increase after full leaf expansion (Isebrands et al. 1994), result from the maturation of non-chlorophyll leaf constituents.

Family was found to affect F_v/F_m, an index reflecting the maximal potential efficiency of PSII, with family 47 having a reduced efficiency relative to families 49 and 97; however, patterns of F_v/F_m response to growth stage remained highly consistent across families. As with other measured physiological patterns, F_v/F_m also responded to growth stage, increasing as the flush progressed to LAG stage, where it reached the highest levels observed in this experiment (Fig. 4).

As was observed for gas exchange parameters, maximal potential efficiency of PSII increased throughout the flush concurrently with the steady decrease in mass-based chlorophyll concentration, providing further indication that chlorophyll synthesis is not a limiting factor with regard to photochemical maturation and photosynthetic efficiency during leaf development of post-transplant northern red oak seedlings. Maxwell and Johnson (2000) attribute alterations in efficiency of non-photochemical quenching as the primary cause of changes in F_v/F_m, implying that observed increases in PSII efficiency during and after leaf expansion may result from the continued synthesis of accessory pigments associated with non-photochemical quenching. F_v/F_m has historically been

employed in stress studies of various *Quercus* species to observe the effects of treatment-induced oxidative stress on PSII, and members of the genus *Quercus* have typically been found capable of maintaining high F_v/F_m values under a variety of adverse conditions (Epron and Dreyer 1992, 1993; Rossini et al. 2006; Sloan et al. 2016). However, inasmuch as the present study demonstrates that endogenous patterns of ontological development can influence patterns of chlorophyll fluorescence, stress studies employing chlorophyll fluorescence measurements should take note of potential confounding effects resulting from interactions between endogenous patterns of seedling development and exogenous stress stimuli.

5 Conclusion

Net photosynthesis, transpiration rate, chlorophyll concentration, and chlorophyll fluorescence depend heavily upon ontological growth stage in post-transplant northern red oak seedlings. Additionally, chlorophyll fluorescence and chlorophyll *a* content were found to vary by family. However, despite variation between families with regard to the values of measured parameters, physiological patterns across growth stages were similar and consistent among half-sibling families. Based on these findings, we conclude that the QMI assumption of consistent physiological patterns across growth stages within a species is likely at least regionally valid with regard to northern red oak. This evidence suggests that use of an appropriate growth index may lead to greater reductions in sources of experimental error than the use of genetically homogeneous plant material.

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Compliance with ethical standards

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