TÜBİTAK

Research Article

Turk J Agric For
35 (2011) 23-30
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doi:10.3906/tar-0908-343

Seasonal changes in the physiological characteristics of Anatolian black pine and the effect on seedling quality

Ayşe DELİGÖZ*

Forestry Faculty, Süleyman Demirel University, 32260 Isparta - TURKEY

Received: 21.08.2009

Abstract: Seasonal changes in water relations parameters, dry weight fraction (DWF), and root growth potential (RGP) were examined for Anatolian black pine [*Pinus nigra* Arn. subsp. *pallasiana* (Lamb.) Holmboe] seedlings. In addition, phenological conditions were monitored. Water relations parameters were estimated using the pressure-volume technique, including osmotic potential at full turgor ($\psi_{\pi 100}$), osmotic potential at turgor loss point ($\psi_{\pi TLP}$), free water content at turgor loss point (FWC_{TLP}), relative water content at turgor loss point (RWC_{TLP}), and symplastic water/dry weight (Vo/DW). $\psi_{\pi TLP}$, $\psi_{\pi 100}$, DWF, and RGP showed seasonal changes, but FWC_{TLP}, RWC_{TLP}, and Vo/DW did not show a clear seasonal change. The osmotic potentials ($\psi_{\pi TLP}$ and $\psi_{\pi 100}$) increased rapidly during rapid shoot elongation, then decreased gradually until autumn, and the minimum values were reached in midwinter. DWF and RGP were highest at the end of January and in mid-February, respectively. The results of the study were discussed based on nursery practices (e.g. lifting and planting time, quality of seedlings) for the species, and as a synthesis of these results, mid-November through mid-March was suggested as the lifting and planting period for bare root Anatolian black pine seedlings.

Key words: Anatolian black pine, dry weight fraction, osmotic potential, root growth potential

Anadolu karaçamı fidanlarının fizyolojik özelliklerindeki mevsimsel değişimler ve bunun fidan kalitesi üzerine etkisi

Özet: Anadolu karaçamı [*Pinus nigra* Arn. subsp. *pallasiana* (Lamb.) Holmboe] fidanlarında su potansiyeli ve bileşenleri, kuru ağırlık oranı ve kök gelişme potansiyelindeki mevsimsel değişimler araştırılmıştır. Ayrıca fenolojik durum gözlenmiştir. Su potansiyelleri ve bileşenleri basınç-hacim eğrisi yöntemiyle tahmin edilmiş ve solma noktasındaki osmotik potansiyel ($\psi_{\pi TLP}$), tam doygun haldeki osmotik potansiyel ($\psi_{\pi 100}$), solma noktasındaki serbest su içeriği (FWC_{TLP}), solma noktasındaki nispi su içeriği (RWC_{TLP}) ve birim kuru ağırlık başına düşen simplastik su miktarı (Vo/DW) belirlenmiştir. $\psi_{\pi 100}$, $\psi_{\pi TLP}$, DWF ve RGP mevsimsel değişimler göstermiştir. FWC_{TLP}, RWC_{TLP} ve Vo/DW'da mevsimsel bir değişim görülmemiştir. Osmotik potansiyeller ($\psi_{\pi TLP}$ ve $\psi_{\pi 100}$) hızlı sürgün uzaması süresince hızla artmış, sonra sonbahara kadar yavaş yavaş azalmış ve en düşük değerlerine kış ortasında ulaşmıştır. DWF ocak sonunda, RGP ise şubat ortasında en yüksek değerleri almıştır. Çalışmanın sonuçları türün fidanlık pratiği açısından (örneğin, söküm ve dikim zamanı, fidan kalitesi) tartışılmış ve elde edilen sonuçların bir sentezi olarak çıplak köklü Anadolu karaçamı fidanları için söküm - dikim zaman dilimi kasım ortası-mart ortası dönemi olarak önerilmiştir.

Anahtar sözcükler: Anadolu karaçamı, kuru ağırlık oranı, osmotik potansiyel, kök gelişme potansiyeli

* E-mail: ayseis@orman.sdu.edu.tr

Introduction

Anatolian black pine [*Pinus nigra* Arn subsp. *pallasiana* (Lamb.) Holmboe] is currently the most widely used tree species in the reforestation of Turkey because of its economic value. It is widely distributed in various regions of Anatolia that are ecologically quite different and have various soil types. In Turkey, Anatolian black pine forests cover 4.2 million ha, and 1.8 million ha of those forests are unproductive (OGM 2006). Each year, millions of bare root Anatolian black pine seedlings are sent to the field for outplanting. However, often, mortality and poor field performance are attributed to poor seedling quality. A successful plantation establishment depends on the use of high quality seedlings. The seedling quality is usually evaluated over morphological (height, stem diameter, height:diameter, and root:shoot) and physiological (water potential, dormancy, root growth potential, and stress resistance) characteristics (Duryea 1985; Ürgenç et al. 1991; Genç 1992).

Measuring seedling quality can help identify possible crop problems and allow for informed decisions on culturing, lifting, storing, and planting (Haase 2007). For this reason, seasonal changes in the physiological and morphological characteristics of seedlings should be examined, and these characteristics should surely be taken into consideration during cultural treatments (lifting, packing, grading, handling, pruning, storage, transport) and outplanting. For example, lifting should not begin until the seedlings become fully dormant (Burdett and Simpson 1984; May 1984). Hence, seasonal changes of dormancy intensity are important for knowing when seedlings enter true dormancy. Besides, these characteristics have been found to be of key importance in determining field performance potential in many species (Burdett 1979; Ritchie and Dunlap 1980; Ritchie 1984; McKay 1997).

Various methods have been developed to test the seedlings' condition before lifting and planting. Dormancy intensity is determined according to bud condition, the bud break test, the dormancy release index, or estimations of dry-weight fraction (DWF). DWF is used routinely in some Swedish seedling nurseries to determine when to begin lifting (Ritchie 1984). Seedlings planted in reforestation sites are exposed to environmental extremes of, for example, temperature and water availability (Radoglou et al. 2003). The tolerance of water stress is mainly related to osmotic and elastic adjustments (Corcuera et al. 2002). Hence, seasonal changes in osmotic potential may help reveal stress (drought) resistance. The pressure-volume (P-V) curve is routinely used as a method for estimating water relations parameters (Duryea 1985). Root growth potential is used to measure the ability of plants to develop new roots in an optimal environment. RGP may be a predictor of planting performance. New root growth is important for a rapid resumption of water and mineral uptake after outplanting (Ritchie 1985).

The objective of this study was to determine the seasonal changes in the physiological characteristics of Anatolian black pine seedlings and to discuss the seedling quality of the species. In addition, the most suitable lifting and planting time for the species was investigated according to the physiological characteristics.

Materials and methods

Seedling material

Anatolian black pine [*Pinus nigra* Arn. subsp. *pallasiana* (Lamb.) Holmboe] seedlings (origin: Eğirdir, Isparta, Turkey) were grown as bare root stock (1 + 0) at a forest nursery (37°53′N, 30°52′E) that is close to the seed stand of the species used in the study.

Phenological conditions

To determine the relationship between physiological and phenological characteristics, 50 seedlings were sampled from a nursery bed. Seedling height, bud break, and terminal bud initiation were observed in 15-day intervals from the beginning of March to mid-September in 2004. The percentage of the seedlings with terminal bud initiation was determined. Seedling height was measured from the soil surface to the tip of the terminal bud.

Water relations

Water relations parameters of shoots were measured by the pressure-volume (P-V) curve using a pressure chamber (Scholander et al. 1965). From April 2004 until March 2005, throughout 1 year, 8 seedlings were randomly lifted from nursery beds at about 15-day intervals. At each lifting time, shoots from each seedling were excised at the root collar and weighed for fresh weight (FW). Shoot samples were kept in distilled water for 24 h in the dark for full hydration, and then shoot samples were weighed for turgid weight. Shoot samples were placed into the pressure chamber and the balance pressures were measured. If the pressure was lower than -0.15 MPa, it was indicated that the shoot was not at full turgor; it was discarded and another sample was selected. Chamber pressure was gradually increased at the same rate as before to 0.3 MPa and was kept at that level for 10 min. Three turgid shoot samples were used and P-V curves were generated as described by Ritchie (1984). The P-V curves were used to estimate osmotic potential at full turgor ($\psi_{\pi 100}$), osmotic potential at turgor loss point ($\psi_{\pi TLP}$), free water content at turgor loss point (FWC_{TLP}), relative water content at turgor loss point (RWC_{TLP}), and symplastic water/dry weight (Vo/DW) (Tyree and Hammel 1972; Ritchie 1984; Genç 1992; Garriou et al. 2000; Mena-Petite et al. 2001).

Dry-weight fraction (DWF)

The dry-weight fraction of seedling shoots was assessed as described by Ritchie (1984). From April 2004 to March 2005, throughout a 1 year period, 10 seedlings from nursery beds were lifted randomly at approximately 15-day intervals. The seedlings were excised at the root collar and shoots were washed in tap water; then the shoot samples were kept in distilled water for 24 h in the dark for full hydration. At the end of this period, the shoot samples were weighed for turgid weight (TW) and the shoots were dried in an oven at 105 °C for 24 h to determine the shoot dry weight (DW). DWF was estimated as: DWF = DW/TW (Ritchie 1984).

Root growth potential (RGP)

RGP was tested using Burdett's method (1979). The seedlings were lifted in approximately 30-day intervals from October 2004 to April 2005. The root growth potentials for seedlings lifted in April were determined after a 10-day cold storage period (at 3 °C), because of early lifting. After washing the roots of each seedling, the root system was pruned to approximately 18 cm below the root collar, and white roots were removed. After pruning, 40 seedlings, 10 seedlings in each replication, were planted in plastic pots filled with a mixture of Anatolian black pine humus and perlite (1:1 by volume). After being watered to the point of saturation, the plastic pots were placed in a controlled environment chamber (day: 30 °C, 16 h; night: 25 °C, 8 h; 75% relative humidity; 25,000 lx from fluorescent). After 1 week, the seedlings were carefully lifted and new roots were assessed according to the method of Burdett (1979). The number of new roots (>1 cm long) was determined.

Statistical analysis

The height growths of 50 seedlings were determined for each measurement date. The ratio of breaking buds to new terminal bud initiation was calculated. The effects of lifting date on water relations parameters, DWF, and RGP were assessed by analyses of variance. Significant differences between variable means were determined by Duncan's multiple range tests. Before the analyses, arcsine transformation was performed for DWF and square-root transformation was performed for root numbers. After transformations, analysis of variance (ANOVA) was applied for the characteristics in the SPSS computer software package (Kalıpsız 1981).

Results

Phenological condition

None of the seedlings showed a sign of bud break until early March. The terminal buds rapidly broke from early March to mid-March. In this period, the seedlings entered the postdormancy term. In early April, 58% of the seedlings broke their buds and 42% of the seedlings entered the growth season. In this period, the average measured seedling height was 3.8 cm (Figure 1). The rapid height increase continued until early May. Terminal bud initiation appeared with a green color in early May and then turned a tile red color for 88% of the terminal buds in early June. The seedlings entered the dormancy initiation term after early June. The dormancy initiation term continued until early September. In early September, the average seedling height was measured as 7.6 cm, and height growth had almost stopped.

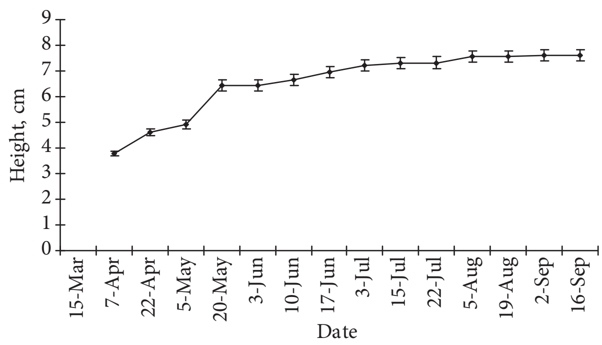

Figure 1. Height growth of seedlings in nursery beds in 2004. Points and bars correspond to means and their standard errors, respectively.

Seasonal changes in water relations

The osmotic potentials at full turgor and the turgor loss point ranged from -0.73 to -1.69 MPa and from -1.73 to -2.99 MPa, respectively (Table 1). Both osmotic potentials showed seasonal variation. The differences among measurement dates were significant ($P < 0.05$) for both osmotic potentials (Table 1). $\psi_{\pi TLP}$ was at higher levels in April and May, and then decreased gradually until autumn. In midwinter (December 30), it had the lowest levels, and then it was again higher in early spring. In the same way, $\psi_{\pi 100}$ showed similar changes, but it was higher by -1.2 MPa compared to $\psi_{\pi TLP}$. FWC_{TLP} and

Table 1. Seasonal changes in osmotic potential at full turgor ($\psi_{\pi 100}$), osmotic potential at turgor loss point ($\psi_{\pi TLP}$), free water content at turgor loss point (FWC_{TLP}), relative water content at turgor loss point (RWC_{TLP}), symplastic water/dry weight (Vo/DW) and dry weight fraction (DWF).

Date	***$\psi_{\pi TLP}$ (-MPa)***	***π_{100} (-MPa)***	***FWC_{TLP} (%)***	***RWC_{TLP} (%)***	***VO / DW (%)***	***DWF***
	Mean ± SE[1]	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**	**Mean ± SE**
14 -Apr-04	1.82 ± 1.33 ab[2]	0.96 ± 0.96 abcd	50.88 ± 4.82 abcdefg	81.33 ± 1.03 abc	1.01 ± 0.082 de	0.30 ± 0.006 b
28-Apr-04	1.79 ± 0.29 a	0.97 ± 0.15 abcd	54.23 ± 1.78 bcdefg	80.08 ± 0.67 ab	1.30 ± 0.066 e	0.27 ± 0.006 a
14-May-04	1.80 ± 1.43 a	0.83 ± 0.52 ab	45.99 ± 2.50 abcde	81.64 ± 2.80 abc	1.03 ± 0.240 de	0.27 ± 0.003 a
26-May-04	2.03 ± 1.51 abcd	1.02 ± 1.47 abcde	52.05 ± 3.76 abcdefg	81.88 ± 2.90 abc	1.00 ± 0.115 de	0.27 ± 0.003 a
10-Jun-04	1.73 ± 1.70 a	0.90 ± 1.39 abc	52.49 ± 4.04 abcdefg	84.35 ± 1.23 abcd	0.92 ± 0.045 cde	0.29 ± 0.003 b
23-Jun-04	1.89 ± 3.49 abc	0.90 ± 2.16 abc	48.99 ± 5.70 abcde	87.21 ± 1.39 cd	0.64 ± 0.121 abcd	0.29 ± 0.003 b
8-Jul-04	2.36 ± 1.23 abcdef	1.07 ± 1.61 abcde	48.21 ± 2.75 abcde	84.97 ± 3.47 abcd	0.75 ± 0.152 abcd	0.29 ± 0.005 b
22-Jul-04	2.21 ± 3.03 abcde	0.95 ± 1.03 abcd	49.94 ± 1.71 abcdefg	90.14 ± 1.46 d	0.47 ± 0.060 ab	0.31 ± 0.003 c
5-Aug-04	2.24 ± 1.40 abcde	1.18 ± 1.17 abcdef	55.78 ± 4.21 bcdefg	86.24 ± 0.95 abcd	0.71 ± 0.120 abcd	0.32 ± 0.005 cd
19-Aug-04	2.49 ± 0.51 cdef	1.34 ± 0.84 bcdef	56.81 ± 1.20 cdefg	83.34 ± 1.81 abc	0.78 ± 0.103 abcd	0.33 ± 0.002 cd
2-Sep-04	2.47 ± 0.54 bcdef	0.98 ± 3.00 abcde	49.74 ± 1.31 abcdef	84.79 ± 1.67 abcd	0.77 ± 0.209 abcd	0.33 ± 0.004 cd
16-Sep-04	2.40 ± 1.16 abcdef	1.29 ± 2.73 abcdef	52.67 ± 9.70 bcdefg	85.00 ± 1.85 abcd	0.77 ± 0.193 abcd	0.33 ± 0.003 d
30-Sep-04	2.55 ± 1.86 cdef	1.69 ± 1.39 f	67.10 ± 3.63 g	79.53 ± 1.84 a	1.04 ± 0.075 de	0.32 ± 0.005 cd
14-Oct-04	2.56 ± 1.13 cdef	1.53 ± 1.54 ef	62.74 ± 2.19 efg	82.89 ± 3.78 abc	0.84 ± 0.129 bcd	0.35 ± 0.003 e
21-Oct-04	2.56 ± 1.78 cdef	1.48 ± 1.72 def	63.43 ± 4.49 efg	84.18 ± 0.92 abcd	0.87 ± 0.134 bcd	0.37 ± 0.002 ef
18-Nov-04	2.49 ± 1.37 cdef	1.63 ± 0.54 f	66.60 ± 2.25 fg	82.82 ± 3.35 abc	0.93 ± 0.149 cde	0.36 ± 0.002 ef
2-Dec-04	2.56 ± 5.51 cdef	1.36 ± 3.30 bcdef	53.77 ± 7.04 bcdefg	87.62 ± 3.57 cd	0.54 ± 0.256 abc	0.37 ± 0.004 fgh
16-Dec-04	2.77 ± 0.03 ef	1.02 ± 0.95 abcde	38.32 ± 2.80 ab	84.28 ± 1.78 abcd	0.43 ± 0.067 ab	0.36 ± 0.003ef
30-Dec-04	2.99 ± 1.03 f	1.50 ± 1.01def	58.08 ± 2.31 defg	86.09 ± 2.63 abcd	0.55 ± 0.118 abc	0.37 ± 0.010 fg
25-Jan-05	2.86 ± 0.36 ef	1.22 ± 1.43 abcdef	41.76 ± 6.76 abcd	87.06 ± 0.77 cd	0.36 ± 0.070 a	0.38 ± 0.003 h
18-Feb-05	2.79 ± 0.42 ef	1.41 ± 1.06 cdef	58.20 ± 2.06 defg	84.67 ± 0.28 abcd	0.63 ± 0.052 abcd	0.38 ± 0.003 gh
5-Mar-05	2.40 ± 2.04 abcdef	0.73 ± 2.39 a	39.32 ± 7.94 abc	81.39 ± 3.56 abc	0.54 ± 0.059 abc	0.36 ± 0.009 ef
16-Mar-05	2.66 ± 0.53 def	1.34 ± 1.07 bcdef	52.48 ± 3.19 abcdefg	81.37 ± 0.29 abc	0.66 ± 0.034 abcd	0.37 ± 0.004 fgh
7-Apr-05	2.52 ± 3.59 cdef	0.81 ± 1.50 ab	36.05 ± 4.90 a	86.56 ± 1.31 bcd	0.35 ± 0.031 a	0.37 ± 0.003 fg
P-Values	**<0.001**	**<0.01**	**<0.05**	**<0.05**	**<0.001**	**<0.001**

[1] SE: standard errors

[2] Different letters indicate significant differences among lifting dates.

RWC_{TLP} ranged from 36.05% to 67.10% and from 79.53% to 90.14%, respectively. Vo/DW ranged between 0.35 and 1.30 (Table 1). There was no apparent seasonal change in FWC_{TLP}, RWC_{TLP}, or Vo/DW.

Seasonal changes in dry-weight fraction

The differences in DWF among measurement dates were statistically significant ($P < 0.001$). DWF decreased during shoot elongation (from mid-April to mid-May; measured as 0.29 and 0.27, respectively), then increased with time and reached its highest value in late January (0.38). DWF decreased again after mid-February (Table 1).

Seasonal changes in root growth potential

Measurement dates had a significant effect on RGP ($P < 0.001$). RGP increased from mid-October to late January and reached its highest level in mid-February. It was low again after February and the lowest in April (Figure 2). The percentage of seedlings that regenerated roots increased from October to November (from 17.5% to 50%) and decreased in December (42.5%). It later increased again and reached 65% in January and February. The percentage of seedlings that regenerated roots reached the highest level, 67.5%, in March. This value decreased to 25% in April (Figure 2).

Discussion

In trees, shoot water potential may fluctuate seasonally (Ritchie and Shula 1984). The changes in the Anatolian black pine seedlings' water relations parameters were closely related to the period of shoot development. $\psi_{\pi 100}$ and $\psi_{\pi TLP}$ values showed seasonal changes. $\psi_{\pi TLP}$ was high when the rates of shoot elongation were rapid. It then declined with time following bud initiation and the minimum values were reached in midwinter, but the values later increased again following the swelling and breaking of terminal buds. FWC_{TLP}, RWC_{TLP}, and Vo/DW displayed no apparent seasonal change. Similar seasonal changes in $\psi_{\pi TLP}$ were determined for *Pinus nigra* subsp. *pallasiana* by Dirik (1999), *Pinus brutia* by Dirik (1991), *Cryptomeria japonica* by Doi et al. (1986), *Pseudotsuga menziesii* by Ritchie and Shula (1984), *Picea glauca* by Colombo and Teng (1992), and *Picea orientalis* by Semerci (1994).

DWF may be used to determine dormancy stage and lifting-planting time (Ritchie 1984). Seedlings are generally considered to be most resistant to handling stresses when dormant (Burr 1990). The stress resistance is closely related to the phenological stage of the seedlings (McKay and Milner 2000; Colombo et al. 2003). In this study, DWF displayed a decrease from early April to late May. Likewise, rapid height increment increase continued until late May. DWF gradually increased after early June. This was the dormancy initiation term, since 88% of terminal buds turned a tile red color in early June. The dormancy initiation term continued until early September, because height growth had almost stopped by then. Dirik (1998) reported that studies on many species (*Pseudotsuga menziesii*, *P. macrocarpa*, *Pinus nigra* subsp. *laricio*, *P. nigra* subsp. *nigricans*, and *Cedrus atlantica*) reported a dormancy initiation term from

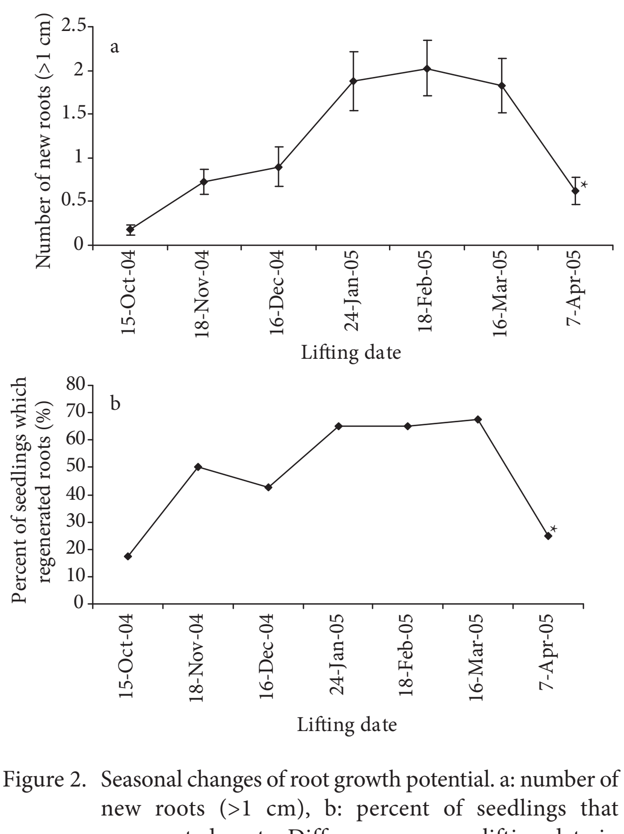

Figure 2. Seasonal changes of root growth potential. a: number of new roots (>1 cm), b: percent of seedlings that regenerated roots. Differences among lifting date in RGP were significant ($P < 0.001$); points and bars correspond to means and their standard errors, respectively. *The seedlings waited in cold storage for 10 days after lifting.

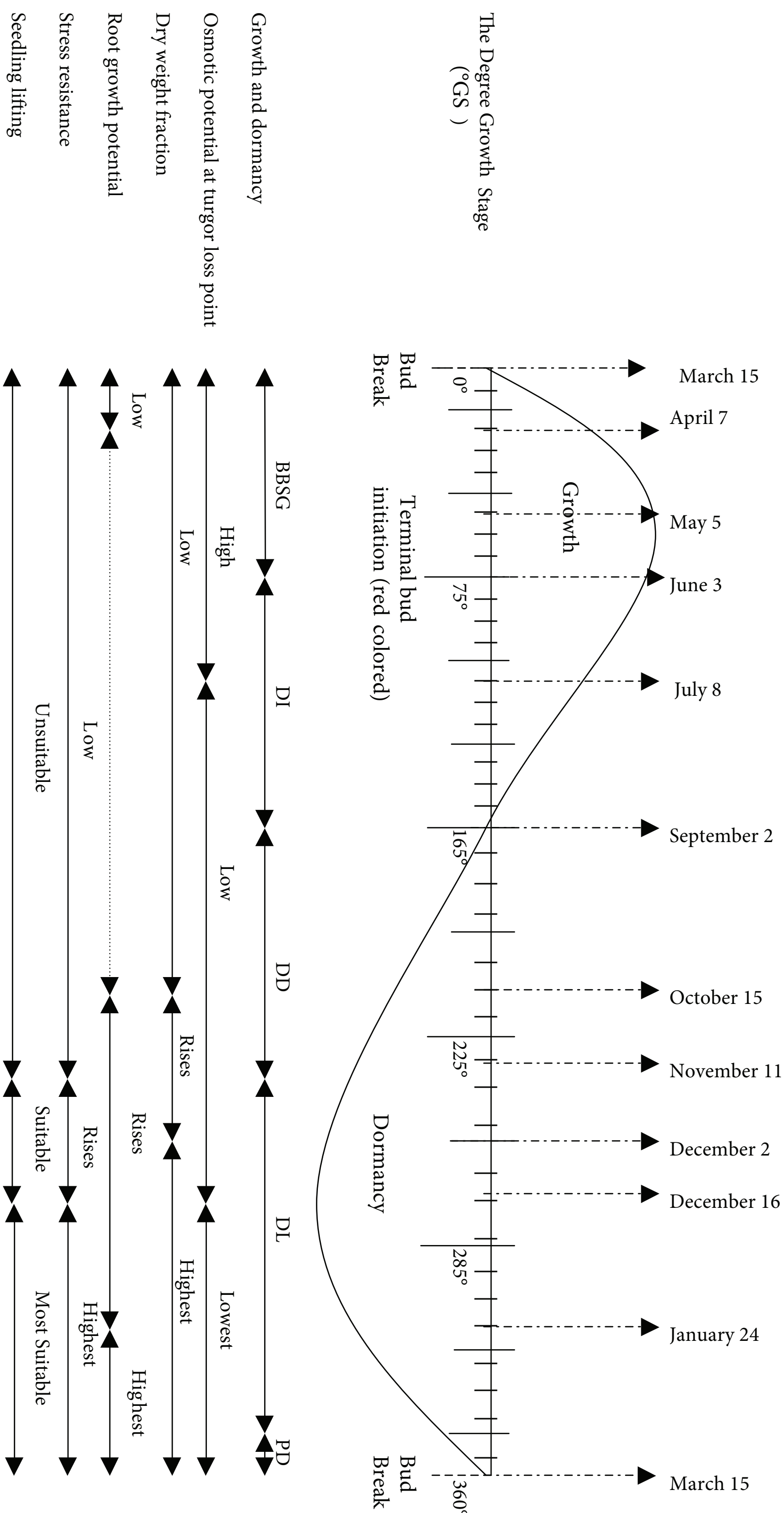

Figure 3. Seasonal changes in osmotic potential at turgor loss point, root growth potential, dry weight fraction, growth, and dormancy status of Anatolian black pine. BBSG: Bud break and shoot growth, DI: Dormancy initiation, DD: Deep dormancy, DL: Dormancy lifting, PD: Postdormancy.

late July to mid-September. Deep dormancy started after early September. The DWF values increased in autumn and were highest in midwinter. This period was determined to be the dormancy lifting term. Additionally, in this period, the osmotic potential turgor loss point decreased with time and was lowest in midwinter. The DWF values again decreased from March onward, because of the broken buds in early March and mid-March. In other words, the seedlings entered the postdormancy term. In conclusion, the DWF values displayed seasonal changes. O'Reilly et al. (2001) determined similar changes in *Larix ′ eurolepis* seedlings. A similar trend was noted by Ritchie (1984). In Douglas-fir seedlings, DWF increases gradually during autumn and early winter, peaks in January, and then falls rapidly during spring. The most suitable lifting period was determined to be mid-November through mid-March, according to DWF (Table 1). Therefore, the dormancy lifting term started in mid-November.

RGP increased from mid-October to late January and reached the highest level in February, followed by lower values again in February, and it displayed the lowest values in April. The percentage of seedlings that regenerated roots was high from October to November, decreased in December, increased again in January and February, and then reached its highest values in March. In summary, the RGP values displayed seasonal changes. Our results on RGP agreed with other studies. For instance, RGP changes may take place in some species during the lifting season, from a low in autumn to a peak in late winter or early spring (Ritchie and Dunlap 1980). Freyman et al. (1986) determined the root growth potential of *Pinus taeda*, which increased through the late autumn and winter, reached a peak in the late winter and early spring, and then declined when bud activity was imminent. Similar changes were determined in *Pinus taeda* by Feret et al. (1985). Dirik (1999) found that the percentage of seedlings regenerating new roots was highest in January, with elevated rates through February and March.

Physiological quality is affected by dormancy or stress resistance status at the time of lifting. Seedlings lifted before or after the period of dormancy lifting are at high risk and are prone to suffer serious damage from cold storage (Ritchie 1984). Ritchie (1986) showed that the time of lifting affects the seedling quality significantly and that seedlings lifted in January showed a higher stress resistance than seedlings lifted earlier or later. The most suitable time for lifting, storing, and planting was at the lowest period of $\psi_{\pi TLP}$, since resistance to drought and frost damage is increased when $\psi_{\pi TLP}$ is low (Dirik 2000). Additionally, both DWF and RGP had high values when $\psi_{\pi TLP}$ was lowest, in midwinter. Especially in February, root growth potential was highest. However, Cleary and Greaves (1979) reported that the root growth potentials of seedling lifting were highest between January and March. Likewise, a study by Garriou et al. (2000) reported that the maximum resistance generally occurs from early winter to midwinter for coniferous and broadleaved species. Planting performance was generally best with seedlings lifted and planted during early winter and midwinter, and poorest for autumn or spring lifting. Considering the values of $\psi_{\pi TLP}$, midwinter (late December through late January) is most suitable for the lifting of Anatolian black pine seedlings in order to have the highest stress resistance, but air and soil temperatures must also be suitable for planting. This resistance is relatively low in autumn (late October through mid-November) and spring (mid-March through early April), because in both of these periods, the values of $\psi_{\pi TLP}$ are relatively high and DWF is decreased. In addition, the seedlings entered the postdormancy term after mid-March. Due to obligatory conditions, if lifting has to be postponed until spring, it must be performed before early April.

In conclusion, when the osmotic potentials, DWF, RGP, and the dormancy stage are evaluated together, the lifting and planting period of Anatolian black pine seedlings should be from mid-November to mid-March (Figure 3).

Acknowledgments

This study was a part of a Ph.D. thesis, prepared under the supervision of Prof. Dr. Musa GENÇ and Hasan ÖZÇELİK and supported by the Scientific and Technological Research Council of Turkey (TÜBİTAK-HD / 105 O 035) and the Süleyman Demirel University Unit of Scientific Research Project (SDÜ - BAP / 936 D 04) Projects.

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