would also yield substantial indirect response in VOL7 but at a considerably lower level.

These results have important implications for a tree improvement program for cottonwood within the sampled area. Predicted genetic gains from clonal selection and propagation were largest when clonal selection was not confined to a subset of stands (Table 6). In addition, predicted gain in growth traits increased with advancing stand development, yielding the largest response to selection (VOL7) at age seven years (Table 6). Due to a large genetic correlation though, selection for DBH4 or VOL4 provides nearly the same level of gain for VOL7 as when selecting directly for it (Table 8). Therefore if increased VOL7 is the goal of selection, a small amount of predicted gain is forfeited (six to seven percent) by selecting for either DBH4 or VOL4 while the length of the testing period is reduced by 43 percent.

The potential exists for selection to improve first year survival (SURV) yet the impact of this trait on VOL7 was low. Clones vary widely for SURV and these problems in initial survival may be due to many factors (COOPER, 1982). The low correlation between SURV and VOL7 may be somewhat misleading when interpolating to volume per unit land area. VOL7 represents the average volume per living tree on a plot basis and therefore does not reflect mortality. Using multiple cuttings per planting spot (with a subsequent thinning to one tree per spot) resulted in very high survival on a plot basis. If planting practices and environmental conditions resulted in significant plot mortality, the correlation between initial survival and volume per unit land area would be important.

Predicted heritabilities and gains are applicable only to sites which are similar to the Fitler test site. Genotype × environment interaction can be important when testing cottonwood in diverse environments (RANDALL and MOHN, 1969; RANDALL and COOPER, 1973). For application of results to a range of planting sites, heritabilities and gains would have to be reduced appropriately for genotype × environment interaction.

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Genetic Variation in Dormancy Relations of Balsam Poplar Along a Latitudinal Transect in Northwestern Ontario

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Summary

Dormancy relations of balsam poplar clones from five populations along a transect from northern Wisconsin to Hudson's Bay were examined in a forcing study. The material exhibited unconditional physiological dormancy in autumn but required a relatively short chilling period to overcome this dormancy. Most of the variance in response to chilling was due to differences among clones within populations. Bud break was promoted by a range of temperatures which were equally effective in terms of response to degree hours.

Key words: chilling requirements, clones, bud break.

Zusammenfassung

In einem Treibhausversuch wurde die relative Winterruhe von Balsampappel-Klonen aus 5 Populationen entlang einer Linie vom nördlichen Wisconsin bis zur Hudson Bay untersucht. Das Stecklingsmaterial zeigte eine uneingeschränkte physiologische Ruhepause im Herbst, erforderte jedoch eine relativ kurze Frostperiode, um diese Ruhepause zu überwinden. Der größte Teil der Variation in der Reaktion auf Frostbedingungen war auf Unterschiede zwischen den Klonen innerhalb der Populationen zurückzuführen. Der Knospentrieb wurde durch einen Temperaturbereich begünstigt, der zeitlich genauso effektiv war, d. h. wie die Reaktion auf die Anzahl Stunden.

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Introduction

Dormancy of North American forest trees has been most frequently examined within the context of provenance in-

vestigations. In this work, genetic variances in dormancy characteristics are considered in relation to natural environmental gradients to which species have adapted phenologically. Evidence for genetic variance in dormancy relations comes from observations of spring growth initiation in field tests (e.g. KRIEBEL 1957, CLAUSEN and GARRETT 1969, MORGENSTERN 1969a, b, BEY 1972, WORRALL 1983) and from studies of growth response after various periods of chilling, i.e., forcing studies (e.g. NIENSTAEDT 1966, FARMER 1968, 1975, CAMPBELL and SUGANO 1979). In eastern deciduous species and some conifers, dormancy appears to fit the model proposed by SMITH and KEFFORD (1964) in which there is a clear distinction between three phases of the bud development cycle: physiological dormancy, imposed dormancy, and steady state shoot growth. Genetic variation in bud break observed in field tests at latitudes above about 40° N is probably related to differences in response to spring temperatures, since chilling requirements have usually been completed by late winter. On the other hand, variation in bud break noted in typical forcing studies may reflect both genetic differences in physiological dormancy (i.e., chilling requirements) and response to forcing conditions.

Genetic variation in the relationship between chilling and bud break may be usefully investigated in light of LEVINS' (1969) hypothesis which considers dormancy as an evolutionary response to environmental uncertainty. According to this hypothesis, in regions characterized by frequent variation in winter temperature above and below 0° C, a species would be expected to develop deep physiological dormancy coupled with cold hardiness. Thus chilling requirements would be high for populations in these places and times, and physiological dormancy might be unconditional in the sense that long photoperiods and/or high temperatures cannot be substituted for chilling requirements. Unconditional physiological dormancy would be expected during periods of environmental uncertainty leading into intolerable conditions (e.g. autumn in the northern hemisphere). During spring uncertainty, unconditional physiological dormancy has no utility, and a plant population must rely on one or more of the following components of frost hardiness: (1) general tolerance of growing shoots to freezing temperatures, (2) variance in susceptibility of

these shoots to cold, or (3) a much delayed shoot growth response to spring temperatures. In climatically milder regions or in areas characterized by a short winter and early spring such a delayed bud break may be related to chilling requirements since periods of true imposed dormancy are brief or lacking. However, in a northern continental climate it is useful to consider genetic variation in chilling requirements and timing of spring growth renewal separately.

Most of balsam poplar's, Populus balsamifera L., range is in continental areas characterized by clearly defined summer and winter divided by brief periods of temperature uncertainty in fall and spring. In such an environment one would expect the species to exhibit unconditional physiological dormancy for a relatively brief period in fall and early winter and little geographic variation in chilling requirement. Since it begins shoot growth relatively early in the spring, balsam poplar would be expected to be frost tolerant after bud break and/or to exhibit a high degree of within-population variance in time of bud break. We have observed that in higher latitudes (50° N +) balsam poplar begins spring growth under generally cooler conditions than material in the southern part of its range. Worrall (1983) has observed that balsam poplar of Yukon origin begins growth near Vancouver, British Columbia much earlier than local black cottonwood, P. balsamifera var. trichocarpa (TORR. et GRAY) BRAYSHAW. One might therefore expect that northern material would have a lower degree-day requirement and/or lower threshold temperature and thus begin growth earlier than southern provenances if both were grown in a common environment. In this forcing study we examined balsam poplar's chilling requirements and flushing pattern in light of the above hypotheses using experimental material taken along a latitudinal transect at Long. 90° W from northern Wisconsin to Hudson's Bay, a distance of about 1200 Km.

Methods
Material

Between 1982 and 1984, cuttings were taken from about 50 seedling ortets in each of five geographical locations (Table 1) on a latitudinal transect from northern Wisconsin

Table 1. — Bud break characteristics of balsam poplar of four provenances after four chilling periods. Test No. 1.

Geographical Source	5–15 °C				10–20 °C				20–30 °C			
	Oct 10	Dec 1	Jan 20	Mar 21	Oct 10	Dec 1	Jan 20	Mar 21	Oct 10	Dec 1	Jan 20	Mar 21
Days to Bud Break												
Wisconsin, 45–46°N												
Mean	26[1]/	21	6	1	32[1]/	14	4	1	[1]/ 32–dor	9	2	1
Range of clone means	20–30	16–29	4–10	0–2	23–43	11–17	2–5	0–2		6–14	1–4	0–2
Thunder Bay, 48–49°N												
Mean	25	22	7	1	31	15	5	3	34–dor	10	5	2
Range of clone means	21–31	17–26	4–10	0–3	24–34	12–18	2–6	0–10		5–14	2–11	0–3
Pickle Lake, 50–51°N												
Mean	25	21	7	<1	25	14	4	1	36–dor	8	3	2
Range of clone means	16–32	17–24	3–9	0–1	18–32	9–18	2–6	0–3		4–13	1–4	0–3
Bearskin Lake, 53–54°N												
Mean	25	21	5	1	29	14	4	1	35–dor	9	3	1
Range of clone means	21–30	16–27	0–14	0–4	21–37	9–19	0–7	0–2		7–11	0–10	0–5
Degree Hours to Bud Break												
All Sources												
Mean		5100	1500			5130	1530			5400	1950	
Range of clone means		3840	0			3240	0			2400	0	
		6960	2400			6840	2520			8400	6600	

1/ All plants forced initially on October 10 were subsequently chilled from November 20 to December 20, then forced again. See text.

to the southwestern shore of Hudson's Bay. In addition to the photoperiod difference along the 1200-Km transect, there is a gradual decrease in mean annual growing degree days above 5.5^0 C from about 1400 in northern Wisconsin to 550 at Ft. Severn on the coast of Hudson's Bay (HARE and THOMAS 1979). Annual mean daily temperature ranges from about 4^0 C at the Wisconsin location to -6.0^0 C at Ft. Severn, and the average mean daily summer (June, July, August) temperature varies from 16^0 C at the southern end of the transect to 10^0 C at the northern end (Environment Canada 1982). There are about 90 frost free days at three central locations, around 100 in northern Wisconsin and 70 near Hudson's Bay (HARE and THOMAS 1979, VISHER 1954). Thus while there is a gradual decrease in average temperature from south to north, the locations in the central portion of the transect have similar frost free periods.

Ortets in each location were at least 1 km apart to minimize the possibility of selecting ramets from a single naturally occurring clone. With the exception of this constraint ortets were randomly selected from populations adjacent to roads or rivers. Populations from northern Wisconsin to the Bearskin Lake area were collected in the summer of 1982 and the early spring of 1983; the Ft. Severn population was sampled in the spring of 1984.

Cuttings were rooted in containers then transplanted to a nursery and/or to large (6 liter) plastic pots. Material for Test No. 1 was propagated from new shoots on these original ramets; the greenwood cuttings were rooted under mist. Material for Test No. 2 consisted of dormant cuttings taken from the nursery in March 1984, or, in the case of Ft. Severn material, dormant cuttings taken directly from juvenile ortets in April 1984. Since nursery and potted plants used in these tests were well established when cuttings were taken, effects of ortet age and environmental preconditioning were minimized and cuttings were physiologically similar for all plants in a single test, except possibly the Ft. Severn material in Test No. 2.

Test No. 1

This test was designed to (1) determine the amount of chilling required to allow shoot growth of balsam poplar, (2) evaluate the effects of a range of alternating temperature regimes on this bud break and (3) make a preliminary assessment of variance in bud break time within and between the several sampled populations. Six randomly selected clones from each of the populations (less Ft. Severn) were expanded via softwood cuttings in early summer 1983, and grown in large Spencer-Lemaire containers ("45's") during late summer. They were moved out-of-doors to natural photoperiods in mid-August. At this time they were arranged into 24 replications of one ramet from each of the 24 clones. On October 10, two replications were placed in each of the following three alternating temperature regimes: 5—15^0 C, 10—20^0 C, 20—30^0 C. The remainder of the replications were placed in a walk-in cooler set at 3—4^0 C. On December 1, January 20, and March 21, six replications were removed from cold storage and two were placed in each of the three temperature regimes. Regimes were established in Model E7 Conviron chambers programmed for 16 hour photoperiods, 4 hours at the highest temperature, 4 hours at the lowest and two-hour periods at 2^0 C steps between.

Plants were observed daily, and the date on which growth of at least one bud was renewed was recorded for each plant. A bud was classified as growing when leaves protruded from the bud tip for at least 2 mm. With the exception of a few plants with damaged apices, growth began with the apical bud.

Days from forcing date to bud break were determined from the above observations and subjected to a factorial analysis of variance which evaluated effects of chilling time, forcing regime, geographical source, and clones within sources.

Test No. 2

Results from Test No. 1 suggested that, though six clones per source was an adequate sample for observing general chilling and temperature effects, it was not large enough to assess provenance differences accurately. Therefore, a second test was conducted in 1984—85, which included a larger sample evaluated in a single forcing environment during the transition period from unconditional to imposed dormancy.

Eighteen to twenty randomly selected clones from each of the five provenances were propagated from dormant cuttings in the spring of 1984, and grown out-of-doors in Spencer-Lemaire containers ("45's"). Nine replications of single ramets were assembled from this material in September. Plants were chilled out-of-doors in an area protected from wind. By November 5, December 5, and January 4, plants had been exposed respectively to 40, 70 and 100 days with minimum daily temperature below 5^0 C. On these dates three replications of material were moved to a greenhouse which had a 16-hour photoperiod and temperatures ranging diurnally from 10^0 to 20^0 C. Dates of bud break were recorded as in Test No. 1.

Results

Test No. 1

All plants forced on October 10, 1983, after exposure to approximately 17 days with mean temperature below 10^0 C, failed to break bud by November 20, at which time they were moved to the walk-in cooler (3—4^0 C). They remained there until moved to growth chambers on December 20. Plants placed in the 5—15^0 C and 10—20^0 C chambers responded to this second forcing period by breaking bud in 20 to 43 days, depending on clone *(Table 1)*. Only 70 percent of plants forced at 20—30^0 C during both periods broke buds, and then only after periods of 21 to 62 days. It is also noteworthy that plants returned to 5—15^0 C began growth sooner than those returned to 10—20^0 C.

Plants forced in December, January and March all initiated normal shoot elongation. Rapidity of response increased from the December sample to the March sample, in which most of the plants had broken bud when removed from cold storage *(Table 1)*. Time to bud break from forcing date was approximately halved by the increase in temperature from 5—15^0 C to 20—30^0 C for December and January samples. Since many of the plants in the March sample were breaking bud on the forcing date, a temperature comparison is inappropriate for this date.

Time to bud break in the three temperature regimes was also examined in terms of degree hours. The 5—10^0 C regime produced 240 degree hours above 0^0 C daily, the 10—20^0 C regime 360, and the 20—30^0 C regime 600. The number of degree hours between forcing date and growth was similar in all three temperature regimes *(Table 1)*, with about 5100—5400 hours required for plants forced in December and 1500—1900 for those forced in January.

Analysis of days to bud break for December and January indicated that temperature and clones within geographical source were statistically significant (.05 level) sources of

Table 2. — Time to bud break of balsam poplar of five provenances after three chilling periods. Test No. 2.

Geographic Source	Percent Plants Breaking Bud, Nov. 5 Sample	Days to Bud Break From:		
		Nov. 5	Dec. 5	Jan. 4
Wisconsin, 45-46°N				
Mean	63 a[1]	43+[2]	17 ab	14 ab
Range of Clone Means	0-100	16-dormant	12-21	11-19
Thunder Bay, 48-49°N				
Mean	72 a	54+	19 a	15 a
Range of Clone Means	0-100	32-dormant	12-27	11-22
Pickle Lake, 50-51°N				
Mean	85 ab	47+	17 ab	13 ab
Range of Clone Means	0-100	27-dormant	13-24	10-17
Bearskin Lake, 53-54°N				
Mean	88 b	36+	15 bc	12 b
Range of Clone Means	33-100	21-dormant	11-22	9-16
Ft. Severn, 55°N				
Mean	100 b	27	14 c	12 b
Range of Clone Means	---	16-51	9-19	8-20

[1] Geographic source means with different letter suffixes are significantly different at the .05 level of probability.

[2] Means for sources from Wisconsin to Bearskin Lake are incomplete since some plants remained dormant for a 12-week period following Nov. 5.

variance. As is apparent from means in *Table 1*, geographical source did not influence time of bud break.

Test No. 2

During a 90 day forcing period after November 5, only part of the plants in this initial sample broke bud, and there was a significant increase in percentage of bud break from southern to northern provenances *(Table 2)*. In the November sample at least one or two clones from each of the three southernmost provenances remained completely dormant on February 5. Therefore the average number of days from forcing to bud break *(Table 2)* is based upon only those clones which began growth. Analysis of variance in days to bud break was not completed since some clones remained dormant. However, results from this sample demonstrate substantial genetic variation in dormancy within as well as among provenances.

Time to bud break decreased from the November sample to the January sample, in which all clones began growth in from 9 to 22 days. In both December and January samples there was a significant decrease in time to bud break from southern to northern material, though the difference was only three days by January. Geographical source accounted for 19 and 12 percent of variance in time to bud break, and clones within sources accounted for 42 and 48 percent of variance in December and January samples respectively.

Discussion

As predicted by our hypothesis, the balsam poplar examined in this test exhibited unconditional autumn dormancy which was overcome by a relatively brief chilling period. By early February all plants were largely in a state of imposed dormancy. For a given amount of chilling the response of thes plants was generally more rapid than that of species examined to date in central North America (e.g. ASHBY 1962, ROBERTS and MAIN 1965, NIENSTAEDT 1966, FARMER 1968, 1975, and FARMER *et al. 1975)*. While a formal comparison of chilling out-of-doors with chilling at 3—4° C is not possible with our data, it is evident that by early January, either out-of-door chilling (mostly far below 0° C) or cold storage facilitated growth resumption. Thus this predominantly boreal species has a chilling requirement which is usually overcome by January.

Chilling in autumn and early winter facilitates bud break at a range of temperatures, and about the same number of

degree hours above 0° C are required before observable growth at any of the temperatures used in this study. Thus there was no gradual widening of the range of temperatures at which plants can grow as chilling proceeded (VEGIS 1964). In fact, slightly higher numbers of degree hours occurred before bud break at 20—30° C than at 5—15° C or 10—20° C. However, it was demonstrated that balsam poplar will begin development at 3—4° C if stored at this temperature for five months, a relationship which does support the VEGIS (1964) hypothesis. This latter response may be partly a function of accumulated degree days, since between January 20 and March 21, when bud growth in cold storage was observed, over 4000 degree hours above 0° C accumulated.

The most outstanding feature of observed variation patterns was the high within-population variance in time to bud break. The ecological value of this degree of phenological variation is not clear given the high level of environmental certainty in early winter when maximum potential variation in response to forcing occurs. The clinal geographic trend in days to bud break during this period of transition to imposed dormancy is likewise difficult to interpret in terms of fitness value. This trend may, in fact, be partly an artifact of differences in time of growth cessation due to variation in photoperiodic response. During preparation of plants it was noted that northern (Ft. Severn, Bearskin Lake) material set buds in late summer several weeks before southern (N. Wisconsin) stock. This relationship has also been noted in our nursery and in a provenance test planting in Thunder Bay. Therefore, while all plants were exposed to the same chilling periods. they may have been in different stages of dormancy induction when chilling began.

Thus in contrast to forcing investigations such as that of CAMPBELL and SUGANO (1979) in which bud break patterns in Douglas fir were correlated with current environmental conditions at geographical source, in our study variation did not appear to have much adaptive significance. At least two hypotheses are worthy of consideration in relation to these observations: First, variation in chilling requirement may be genetically correlated with growth cessation and/ or spring bud break patterns which do have current fitness value. In this case one might expect minimal variance between sources and broad within-source variance in bud break time in the central area of our sampled region where the frost free period is about the same and probabilities of late spring and early fall frosts are roughly equal. Second, variation in response to chilling may be a remnant of adaptive characteristics which had more value prior to the post-glacial expansion of balsam poplar's range to its present state. Examination of phenological characteristics of clones in field tests now underway will be useful in evaluating these closely related hypotheses.

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Influence of Age on Sylleptic and Proleptic Free Growth of Norway Spruce Seedlings*)

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Abstract

Shoot growth of young Norway spruce (Picea abies (L.) KARST.) seedlings and the influence of age on two forms of shoot growth: (1) predetermined growth, in which needle primordia develop in the preceding growth period, overwinter in the bud, and elongate in the following spring, and (2) free growth, where needle primordia develop and elongate in the same growth period, were studied. One, two, and four year old seedlings of one provenance were grown under natural daylength conditions to allow free growth, and under short day conditions to prevent free growth. The results show the following trends: with increasing age increasingly larger parts of the shoot elongate in the form of predetermined growth until eventually all shoot growth develops in the form of predetermined growth on an adult tree. With increasing age free growth also changes. Whereas on one hand free growth starts immediately after the termination of predetermined growth and without setting a bud on very young seedlings of about one to three years of age on the other, it continues after setting a temporary bud on seedlings that are still young, but above the age of about three years. Therefore, free growth which starts immediately after predetermined growth is defined as sylleptic free growth (sylleptos = together), and free growth which starts after a temporary bud has been set, as proleptic free growth.

Key words: Picea abies, shoot growth, predetermined growth, sylleptic and proleptic free growth, lammas shoots, morphology of free growth, short day treatment.

Résumé

L'objectif de la présente recherche était d'obtenir de nouvelles connaissances sur la croissance longitudinale de bourgeons de jeunes semis d'épicéa (Picea abies (L.) KARST.) et sur l'influence de l'âge des plantes sur celle-ci. A cet effet furent observées:
1. La croissance prédéterminée où l'initiation des aiguilles date de l'année précédente et où l'allongement s'effectue au printemps après l'hivernage des aiguilles en bourgeon.
2. La croissance libre où l'initation des aiguilles et la pousse tombent en une même période de végétation.

Pour des plantes de deux, trois et quatre ans de même provenance, la croissance libre fut obtenue par une durée de jour naturelle et empêchée par une photopériode journalière réduite. Deux tendances de dévelopment furent constatées en fonction de l'âge augmentant des plantes:
1. La part proportionnelle de la croissance prédéterminée contribuant à la longueur finale augmente, de manière qu'après la phase de jeunesse, la pousse principale repose entièrement sur la croissance prédéterminée.
2. La croissance libre succède immédiatement à la phase de croissance prédéterminée pour ce qui est des semis très jeunes, tandis que pour les semis de, à peu près, trois ans et plus, elle ne s'effectue qu'après une interruption de croissance avec une formation de bourgeon passagère.

La croissance libre succédant immédiatement à la croissance prédéterminée est ici qualifié de 'croissance libre sylleptique' (sylleptos = [avec croissance prédéterminée] intégrée) et la croissance libre se produisant après interruption de la croissance en longueur est désignée 'croissance libre proleptique (anticipée [à l'année suivante]).

Zusammenfassung

Mit dem Ziel, das Trieblängenwachstum junger Fichtensämlinge (Picea abies (L.) KARST.) und den Einfluß des Alters auf das Trieblängenwachstum zu untersuchen, wurden 1.) das prädeterminierte Wachstum, bei dem die Nadelprimordien im Vorjahr angelegt und nach der Überwinterung in einer Knospe im folgenden Frühjahr gestreckt werden und 2.) das freie Wachstum, bei dem die Nadelprimordien in der gleichen Vegetationsperiode angelegt und gestreckt werden, beobachtet. Ein-, zwei- und vierjährige Pflanzen einer Herkunft wurden bei natürlicher Tageslänge wachsen gelassen, um freies Wachstum zu erlauben, und bei Kurztagsbedingungen, um das freie Wachstum zu verhindern. Mit zunehmendem Alter zeigen sich zwei Entwicklungen: 1.) der Anteil des prädeterminierten Wachstums an der Gesamttrieblänge nimmt zu, so daß der Haupttrieb nach der Jugendphase ausschließlich aus prädeterminiertem Wachstum gebildet wird. 2.) Beim freien Wachstum ist zu beobachten, daß es bei sehr jungen Sämlingen unmittelbar auf das prädeterminierte Wachstum folgt, während es bei etwas älteren Sämlingen im Alter von ca. drei Jahren aufwärts häufig erst nach einer Pause im Trieb-